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THE CONDUCTING SYSTEM OF THE BIRD'S HEART

By FRANCIS DAVIES, M.D. (London)

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INTRODUCTION

The existence of a specialised form of muscle tissue connecting the auricles and ventricles of the bird's heart, and analogous with the bundle of His and Kent of the mammalian heart, has been denied by many investigators. Furthermore, there is considerable divergence of opinion regarding its disposition among those who have satisfied themselves of the existence of a special avian conducting system.

Tawara (1), Obermeier (2) and Hofmann (3) found numerous large Purkinje fibres in the ventricles, not only in the sub-endocardial connective tissue but also running into the depths of the myocardium with the larger arteries. Keith, Mackenzie and Robertson (4 and 5) after an extensive investigation of the hearts of Vertebrates came to the conclusion that the auriculo-ventricular bundle, as a specialised strand, is peculiar to Mammals. These authors also deny the existence of sinu-auricular and auriculo-ventricular nodes as specialised structures in the bird's heart, though they noted an intimate association between nerve and muscle in the regions of junction of sinus and auricle and of auricle and ventricle. Kulb (6) found a tract of tissue in the bird's heart, resembling in structure the mammalian A.-V. bundle, running across the A.-V. junction at its posterior part and thence prolonged forwards and downwards to join the musculature of the ventricular septum after a short course. Mackenzie (7) found a bundle of "muscle and nerve tissue" passing from the right auricle to the right ventricle only, and Flack (8) showed that when this bundle was ligatured complete A.-V. dissociation occurred. Florence Buchanan's observations on the electro-cardiograms of the bird also suggested that the route of contraction differs in the bird, where the bundle (according to Mackenzie) descends on the right side only, from that in the mammal where the bundle descends on both sides. Mackenzie also found occasional strands of muscular connection between the right auricle and the right ventricle over the free edge of the muscular valve. No such direct muscular continuity was observed on the left side where the parietal valve is membranous and continuity intercepted by a fibrous ring. Mangold and Kato (9) performed a series of cutting and ligaturing experiments at the A.-V. junction of the heart of the fowl and noted the effects produced upon the subsequent electro-cardiograms. They concluded that the following structures are present in the bird's heart: sinu-auricular node near the termination of

the right superior vena cava, and auriculo-ventricular bundle with two terminal branches in the ventricular septum. However, they could find no histological differentiation of any specialised muscle tissue in the above sites. Lewis (10) deduced from his electrical studies of the spread of the excitatory process in the bird's heart that the spread, from its rapidity, must be through a special distributing system as in Mammals, and that the supply of specialised tissue to the right and left ventricles is separate as in the mammalian heart. Tang (11), from his study of the minute structure of the Purkinje fibres in the bird's heart, concluded that they are specially modified parts of the conducting system (Reizleitungssystem) and not, as Retzer (12) asserted in the case of the mammalian Purkinje system, embryonal growth centres for the replacement of cardiac musculature. Clark (13), in discussing the conduction in the bird's heart, states that the Purkinje fibres do not form a definite connecting strand between auricle and ventricle, and that the significance of the large Purkinje fibres in auricles and ventricles for the conduction of excitation is therefore obscure. Drennan (14) made naked-eye dissections of the A.-V. bundle in the ostrich heart. No A.-V. node was seen, though a rich nerve supply from the right coronary plexus was made out in the region of commencement of the bundle. The bundle passed from the posterior part of the base of the auricular septum into the depth of the ventricular septum, where it inclined towards the endocardium on the left side of the septum. Whilst in the ventricular septum the bundle gave off a branch to the muscular valve at the right auriculo-ventricular orifice, this branch the author regards as the homologue of the right limb of the mammalian bundle. Ohmori (15) found the auriculo-ventricular node present in the bird's heart in the lower part of the auricular septum and from it a bundle of specialised muscles passes into the depth of the ventricular septum where it divides into right and left branches which pass to the corresponding sides of the septum. In addition to this main bundle, Ohmori describes "four allied systems" as follows: (*a*) a specialised bundle passing from the A.-V. node to the posterior part of the muscular valve; (*b*) a specialised bundle running from the connective tissue at the root of the aorta through the anterior wall of the right auricle to the free border of the muscular valve where it joins system (*a*), the free border of the valve being regarded as the border line between the right auricle and ventricle, and systems (*a*) and (*b*) forming accessory auriculo-ventricular connections; (*c*) a specialised bundle running from the bifurcation of the main bundle upwards through the ventricular septum to the root of the aorta where it joins system (*b*); (*d*) a peri-arterial collection of Purkinje fibres accompanying the arteries through the ventricular myocardium. Holmes (16) found numerous Purkinje fibres in *both auricles* of many birds, both in the sub-endocardial connective tissue, around arteries in the myocardium and to a slight extent in the epicardium. In the smaller birds' hearts the Purkinje fibres showed only very slight histological differentiation from ordinary cardiac muscle and were recognisable only under high magnification. Holmes is of the

opinion that these fibres do not form the path of conduction of the stimulus to contraction in the auricles.

PERSONAL OBSERVATIONS

The results of the present study are based upon the histological investigation of the hearts of the black swan and pigeon in particular. Serial sections (transverse) of these hearts were examined and special blocks from the hearts of the ostrich, stork, black crake and king penguin were also studied. In view of the failure of Mackenzie and Robertson (4) to find a specialised conducting system in the pigeon heart, and bearing in mind the statement of Holmes (16) concerning the slight degree of differentiation of the auricular Purkinje fibres from the myocardium in the hearts of the smaller birds, it was deemed advisable to feed some pigeons well for some time (ten days) prior to removal of the heart in the endeavour to increase the glycogen content of the special conducting system in the hope that this would render the histological difference between the conducting system and the ordinary cardiac muscle more marked. With this preliminary treatment the special conducting system of the pigeon heart was found to be markedly differentiated from the cardiac muscle. The present work is an attempt at a complete study of the topographical disposition of the avian Purkinje system. An endeavour is also made to correlate the peculiar and intricate detail of this system with the functional requirements of the bird's heart. Finally the conducting system of the avian heart thus determined is compared with the present conception of that of the fish and reptile heart on the one hand and with that of the mammalian heart on the other.

DISTRIBUTION OF THE CONDUCTING SYSTEM IN THE BIRD'S HEART

A. *Specialised connections between auricle and ventricle*

The specialised connections between auricle and ventricle are:

1. Auriculo-ventricular node and bundle;
2. Right auriculo-ventricular ring of Purkinje fibres.

1. *The auriculo-ventricular node* (Plate I, fig. 1) is embedded in connective tissue in the lower and posterior part of the auricular septum, a short distance in front and to the left of the opening of the left superior vena cava, a position similar to that occupied by Tawara's node in the mammalian heart. It is ovoid in shape and its lower and anterior part narrows into the commencement of the A.-V. bundle, though it is difficult to demarcate with certainty where node ends and bundle begins owing to similarity of structure. The lower part of the node consists of cells which are larger than the auricular myocardial cells proper, which do not stain so deeply as the myocardium and in which the longitudinal fibrillae are limited to the periphery. The cells are frequently seen to be multinucleated, the nuclei (usually two in number) being rounded

in shape and central in position. The cells in the lower part of the node are more compactly arranged than those in the upper part. The upper part of the node consists of cells, smaller in size, multinucleated, with longitudinal fibrillae only at the periphery, and arranged in strands which are separated from each other by connective tissue. These strands become directly continuous with the ordinary auricular myocardium, but no direct continuity with the Purkinje fibres of the right auricle was observed. The node is surrounded by connective tissue (which is continuous with the auriculo-ventricular fibrous rings and trigonum fibrosum) in which many blood vessels are embedded. Numerous small ganglia and nerve fibres lie in the epicardium immediately superficial to the nodal region. No nerve cells were seen in the node but many nerve fibres penetrate into the perinodal connective tissue. With the stains employed, viz. haematoxylin and eosin, and van Gieson and iron haematoxylin, nerve fibres are not conspicuous in any part of the avian conducting system, though they may be difficult of recognition, especially if non-medullated. This question is being investigated by the use of special stains and will be dealt with in a later communication.

The auriculo-ventricular bundle (Plate I, fig. 2) commences as a narrow rounded bundle continuous with the lower and anterior end of the A.-V. node in the trigonum fibrosum. It soon broadens out and runs forwards and to the left into the depth of the ventricular septum. Thence it passes downwards, forwards and to the left, deeply embedded in the ventricular septum, to a point slightly below and to the right of the anterior septal attachment of the muscular right A.-V. valve. This site is about one-fifth to one-quarter of the distance from the base to the apex of the ventricular septum, and here the bundle, lying midway between the right and left surfaces of the septum, divides into its two limbs, right and left. The bifurcation of the bundle (Plate I, fig. 4) lies deep to (i.e. on the left side of) the main septal division of the right coronary artery, only a thin layer of septal myocardium intervening between the artery and the bifurcation of the bundle, but no communications could be traced between the Purkinje fibres of the bundle and the collection of Purkinje fibres around the septal artery. The main A.-V. bundle consists of large cells, compactly arranged, with longitudinal fibrillae at the periphery and usually two rounded central nuclei. The cells vary in size in various parts of the bundle, tending to be bigger towards the bifurcation and smaller at the constricted commencement of the bundle. The connective tissue about the A.-V. node is continued around the main bundle only to a very slight extent. There is not the same compact sheath (Plate I, fig. 3) around the avian bundle such as is seen in relation to the mammalian bundle (especially in the hearts of Ungulates). In most of the birds' hearts examined there is no connective tissue at all around the bundle, so that its peripheral fibres lie in direct apposition with the septal myocardial fibres and, indeed, may be seen to pass into direct continuity with them. Blood vessels are scanty in the bundle, its vascularity being much less than

that of the myocardium. Nerve fibres are not conspicuous with the stains employed.

Right limb of the A.-V. bundle (Plate I, fig. 5). From the bifurcation of the main bundle the right limb runs downwards and slightly forwards, at the same time approaching the endocardium on the right side of the septum. It passes in front of and close to the main septal artery, but no fibres appear to pass directly from the right limb to the collection of Purkinje fibres around the artery. At its commencement the right limb is broad, flat and compact, but as it approaches the endocardium it becomes rounded and its component fibres more loosely arranged. After a short course the right limb reaches the sub-endocardial connective tissue on the right side of the septum, where it spreads out (Plate I, fig. 6) and becomes continuous with the sub-endocardial network of Purkinje fibres. The cells of which the right limb consists have the same characters as those of the main bundle, and as in the case of the latter, a connective tissue sheath is absent, the peripheral specialised fibres of the right limb being directly continuous with the neighbouring septal myocardial fibres. Further, as the right limb approaches the endocardium, strands of ordinary myocardial fibres actually pass transversely through the limb between the specialised fibres (Plate II, fig. 7). As it nears the endocardium, the right limb gives off a small rounded branch (Plate II, fig. 8) composed of loosely arranged Purkinje fibres, which runs upwards and to the left immediately beneath the endocardium, to enter the muscular valve at its anterior septal attachment. This is the first branch given off from the right limb and its distribution to the muscular right auriculo-ventricular valve suggests that this valve *actively* contracts *early* in ventricular systole, so allowing exit for the blood from the right ventricle through the pulmonary artery alone during the greater part of systole of the ventricle. As far as the present writer is aware, it is unknown at what exact period of the cardiac cycle this muscular valve comes into operation and it is proposed to investigate this question experimentally. In the exceedingly rapid hearts of small birds it is evident that ventricular systole is of very short duration, and that for transmission of the greater part of the ventricular blood through the pulmonary artery during systole the auriculo-ventricular orifice must be closed almost at the outset of systole. If the above suggestion is correct it represents an interesting example of adaptation of structure to function in the rapidly beating bird's heart. This branch to the muscular valve was described by Drennan (14) in the ostrich, and he regarded it as the homologue of the right limb of the mammalian bundle, but it is clear that it is only a branch of the right limb of the avian bundle, the latter itself being the true homologue of the right limb of the mammalian bundle.

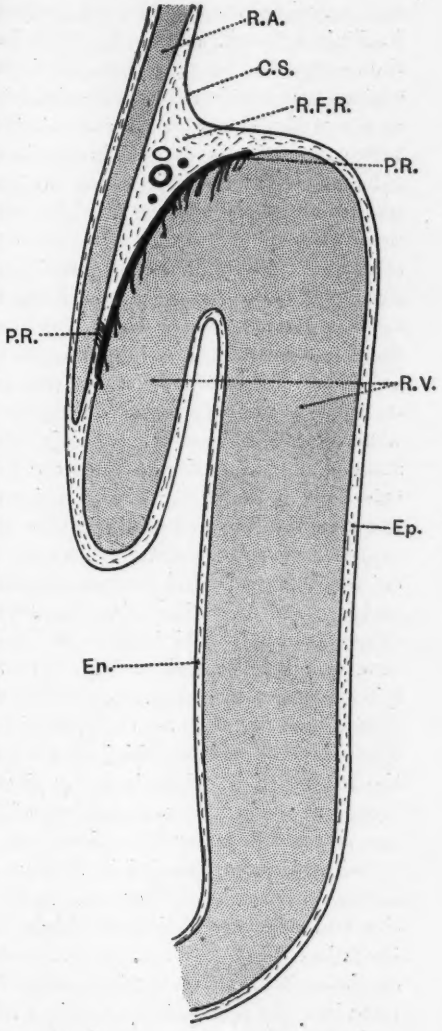
Left limb of the A.-V. bundle (Plate I, fig. 5). From the bifurcation of the main bundle the left limb runs downwards and, after a short course, reaches the sub-endocardial connective tissue on the left side of the ventricular septum (Plate II, fig. 9), where it spreads out to become continuous with the network

of Purkinje fibres beneath the endocardium. From its commencement the left limb assumes the form of a broad flattened band of compactly arranged fibres, but as it approaches the endocardium the fibres become more loosely arranged as they diverge to become continuous with the sub-endocardial Purkinje network. There is no connective tissue sheath around the left limb, the peripheral specialised fibres establishing continuity with the neighbouring myocardium. The cells of which the left limb consists have the same histological characters as those of the main bundle; they tend to get larger as the endocardium is approached. In both right and left limbs, as in the case of the main bundle, blood vessels and (with the stains used) nerve fibres are conspicuous by their absence.

Special recurrent branch of the A.-V. bundle. From the point of its bifurcation the main A.-V. bundle gives off a branch which runs upwards, forwards and to the left in the depth of the ventricular septum (Plate II, fig. 10). It takes the form of a rounded bundle in which the Purkinje fibres are compactly arranged, and about which there is no connective tissue sheath, the peripheral specialised fibres establishing continuity with the neighbouring septal myocardium. The branch rapidly diminishes in size as it approaches the base of the ventricular septum, where it lies in the septal myocardium in front of the mitral orifice. Thence it passes upwards, as a very small bundle, in the myocardium on the anterior and left aspect of the root of the aorta, where it receives communications from the peri-arterial collections of Purkinje fibres about the neighbouring branches of the left coronary artery. Finally it passes backwards (Plate II, fig. 11) in the connective tissue on the left side of the root of the aorta and ends by joining the aortic end of the bundle of Purkinje fibres, which passes from the auriculo-ventricular node around the right auriculo-ventricular orifice, behind the root of the aorta.

2. *Right auriculo-ventricular ring of Purkinje fibres.* A study of the structure of the muscular right auriculo-ventricular valve reveals that it consists chiefly of an inflection of the ventricular myocardium, with a much smaller inner layer of auricular muscle (text-figure 1). The auricular myocardial component of the valve does not reach down as far as the lower free border of the valve in any part of its circumference, but extends downwards on the inner aspect of the ventricular myocardial component for varying distances in different parts of the valve. Between these two myocardial components of the valve there is a collection of fibrous tissue which is really part of the right auriculo-ventricular fibrous ring, the invaginated condition of the muscular and fibrous constituents of the valve having been produced by the upward expansion of the ventricle. From the lower and posterior part of the auriculo-ventricular node (Plate II, fig. 12) a small bundle of Purkinje fibres is given off, which passes at first backwards and to the right, in the right auriculo-ventricular fibrous ring, into the fibrous tissue between the auricular and ventricular components of the muscular valve. In this connective tissue it expands into the form of a sheet of Purkinje fibres (Plate III, fig. 13) which

passes forwards and subsequently to the left, finally leaving the valve by passing into the connective tissue on the right side of the root of the aorta (Plate III, fig. 14). Here it again assumes the form of a small rounded bundle, and inclines backwards to join the aortic end of the recurrent branch of the main auriculo-ventricular bundle in the connective tissue on the back of the root of the aorta. On its way round the right auriculo-ventricular orifice, in the fibrous tissue between the auricular and ventricular myocardial components of the valve (Plate III, fig. 15), this sheet of Purkinje fibres establishes continuity with both auricular and ventricular myocardial parts of the valve, thus constituting accessory auriculo-ventricular connections. This special auriculo-ventricular ring of Purkinje fibres comes into intimate association with the numerous small ganglia and nerve fibres in the connective tissue at the base of the valve. Likewise in the connective tissue at the base of the aorta, the terminal parts of the recurrent branch of the main A.-V. bundle and of the special ring of Purkinje fibres are very intimately related to the ganglia and nerve fibres in this situation.



Text-fig. 1. Diagram of structure of muscular right auriculo-ventricular valve.

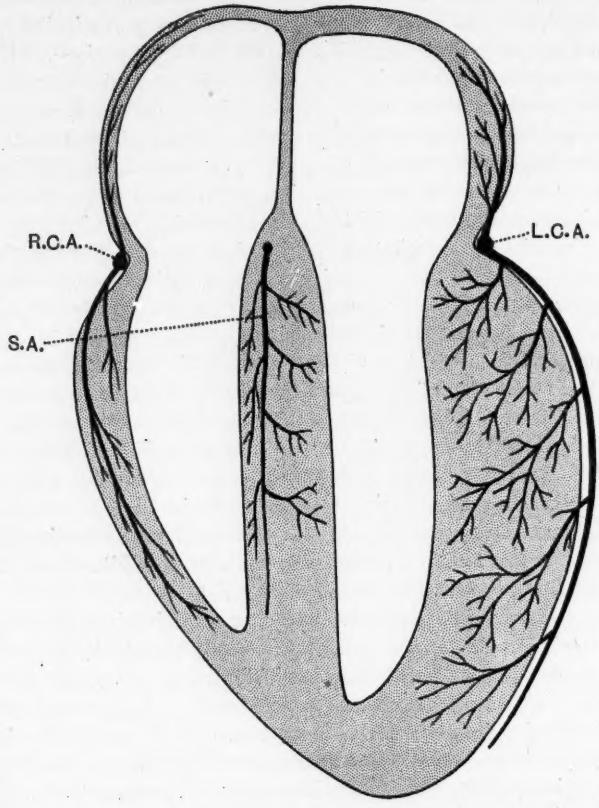
B. *Distribution of the Purkinje fibres in the ventricles*

The Purkinje fibres have a very extensive and intricate disposition in the ventricular walls, being found beneath the endocardium, around arteries in the myocardium, and to a lesser extent in the epicardium. The detailed architecture of this Purkinje system has up to the present remained untraced.

1. *Ventricular sub-endocardial Purkinje fibres.* The right and left limbs of the main A.-V. bundle have been shown above to pass to the sub-endocardial connective tissue on the right and left sides respectively of the ventricular septum, where they spread out and are continued into the sub-endocardial Purkinje network. The fibres of this latter network run downwards towards the apex of the heart, and also radiate to right and left on each side of the septum to reach the sub-endocardial network on the free walls of the ventricles at the region of septal attachment, this arrangement being similar to that which occurs in the case of the *left* limb only of the mammalian bundle. No sub-endocardial Purkinje fibres are found on either side of the ventricular septum above the level at which the right and left limbs of the A.-V. bundle reach the sub-endocardial connective tissue, except at the junction of the septum and free wall of each ventricle, where some of the radiating Purkinje fibres may curve upwards to reach slightly higher than the level of commencement of the network on the septum. On the free wall of the right ventricle the sub-endocardial Purkinje fibres pass up to the attachment of the muscular valve, and also extend for a short distance on to its ventricular surface. They do not form auriculo-ventricular connections over the free border of the valve with the sub-endocardial Purkinje fibres of the right auricle. Only a few sub-endocardial Purkinje fibres are found in the lower part of the conus arteriosus and none at all in its major portion. The sub-endocardial Purkinje fibres on the free wall of the left ventricle run up as far as the attachment of the mitral valve, but stop short some distance from the aortic valve. They are entirely independent of the sub-endocardial Purkinje fibres of the left auricle and form no connections with them. It is to be noted that in most places the sub-endocardial Purkinje fibres lie in contact with the subjacent myocardial fibres proper, the main thickness of the sub-endocardial connective tissue lying between them and the endocardial lining of the ventricles. In many places, however, they are embedded in the sub-endocardial connective tissue. The sub-endocardial Purkinje fibres are most numerous on the free wall of the left ventricle, where in many places they form practically a continuous layer (as seen in transverse sections of the heart) (Plate III, fig. 16). The cells are very much larger than the myocardial cells, and frequently show two nuclei which are rounded in shape and central in position. Longitudinal fibrillae are few in number and are limited to the periphery of the cell. The size and structure of these Purkinje cells markedly differentiate them from the adjacent myocardium. From the sub-endocardial Purkinje network, both on the septum and on the free walls of both ventricles, Purkinje fibres penetrate into the adjacent myocardium and become continuous with either the ordinary myocardial fibres directly or with the peri-arterial collections of Purkinje fibres about the myocardial branches of the coronary arteries. These penetrating strands of Purkinje fibres are especially marked in the free wall of the left ventricle, and arise from the sub-endocardial network chiefly in the sulci between the trabeculae carneae.

2. *Peri-arterial Purkinje fibres in the ventricular walls.* As above described, strands of Purkinje fibres penetrate from the sub-endocardial network into the adjacent myocardium. Most of these penetrating strands become continuous with the collections of Purkinje fibres around the myocardial branches of the coronary arteries (Plate III, fig. 17), and are conducted along these arteries throughout the thickness of the myocardium towards the epicardial surface (Plate III, fig. 18), the fibres on their way establishing continuity with the myocardial fibres at various depths from the surface. All the peri-arterial collections of Purkinje fibres appear to be derived from the sub-endocardial networks in the various regions of the heart wall, and, conducted along the myocardial branches of the coronary arteries, they form an intricate intramyocardial system of conducting fibres, establishing continuity with the ordinary cardiac muscle at numerous sites along their course. In some places the fibres follow the arteries right through the thickness of the myocardium into the epicardial connective tissue, this being especially the case in the free wall of the left ventricle, where peri-arterial Purkinje fibres are found about the main branches of the left coronary artery as they lie in the epicardium in the region of the anterior interventricular sulcus. A clue to the detailed architecture of this intricate peri-arterial Purkinje system is obtained by a study of the "pattern" of the myocardial branches of the coronary arteries in the walls of the various chambers of the heart (text-figure 2). The type of pattern is found to vary with the varying thickness of the cardiac wall. In the case of the very thick free wall of the left ventricle, the descending branches of the left coronary artery, which lie in the epicardium, give off twigs which enter the myocardium at a wide angle and arborise throughout the thickness of the wall in a tree-like manner. In the thinner free wall of the right ventricle, twigs from branches of the right coronary artery enter the myocardium at an acute angle and only gradually sink into the depth of the wall. In the thin walls of the auricles (especially the right) the arteries only very gradually sink into the depth of the myocardium, the smaller twigs running more or less parallel with the surface. In a similar manner the main arteries descending in the ventricular septum lie between a thin right and a thick left layer of the septal musculature, and the branches passing towards the endocardium on the left side of the septum have thus a "tree-pattern" of distribution like those in the thick free wall of the left ventricle, whilst those passing towards the right side of the septum follow a "parallel-pattern" and only gradually pass through the thin right layer of the septum. It is thus evident that in the case of the thick free wall of the left ventricle and of the thick left layer of the ventricular septum the branches of the coronary arteries take a comparatively *short course* through the thick muscular layer. The peri-arterial Purkinje fibres in the ventricular walls are independent of those in the auricular walls and do not afford a means of specialised connections between auricles and ventricles. In the ventricular septum, below the level of the commencement of the sub-endocardial Purkinje networks on either side,

the branches of the septal arteries passing towards the right and left surfaces of the septum are surrounded by Purkinje fibres derived from the right and left sub-endocardial networks respectively. The peri-arterial Purkinje fibres about the main septal artery as it lies in the septum above the level of the bifurcation of the main A.-V. bundle are derived from the sub-endocardial



Text-fig. 2. Diagram of pattern of coronary arteries of bird's heart. (For explanation see text.)

network on the right side of the septum lower down and are passing upwards to become continuous with the myocardium of the upper and right part of the septum. This recurrent arrangement of these peri-arterial Purkinje fibres is comparable to that of the recurrent branch given off from the A.-V. bundle at its bifurcation, many of whose fibres become continuous with the myocardium of the upper and left part of the ventricular septum. As the main septal artery (i.e. the main branch of the right coronary artery) is passing downwards and backwards in the upper part of the ventricular septum, at

the sites where it lies subjacent to the anterior and posterior septal attachments of the muscular valve, it gives off branches, surrounded by Purkinje fibres, to this valve. In the conus arteriosus the peri-arterial Purkinje fibres are derived from the sub-endocardial Purkinje fibres of the adjacent part of the right ventricle, and they are arranged about branches of the third coronary artery. This is the last coronary artery given off from the aorta and it is entirely expended upon supplying the part of the right ventricle that has been shown by Lewis to contract last, viz. the conus.

C. *Distribution of Purkinje fibres in the auricles*

As in the walls of the ventricles, Purkinje fibres have an extensive and complicated arrangement in the auricular walls, and are found beneath the endocardium, around arteries in the myocardium and in some places in the epicardium. Sub-endocardial Purkinje fibres (Plate IV, fig. 19) are found throughout both auricles, but are relatively scarce on the auricular septum. They become less numerous in the lower parts of the auricular walls and stop short some distance above the auriculo-ventricular valves. They do not constitute special auriculo-ventricular connections, but are independent of those in the ventricular walls. As in the case of the ventricular system, branches from the sub-endocardial Purkinje fibres penetrate into the auricular myocardium around the auricular branches of the coronary arteries, and in some places the peri-arterial Purkinje fibres pass through the entire thickness of the auricular wall into the sub-epicardial connective tissue. This auricular peri-arterial system of Purkinje fibres is independent of the ventricular peri-arterial system, and no connections could be traced between them.

Sinu-auricular node (Plate IV, fig. 20). Beneath the epicardium at the base of the right venous valve there is a mass of fibres which does not stain so deeply as the adjacent myocardium. This mass is widest in its middle and tapers off above and below. It extends upwards from just above the orifice of the inferior vena cava to a point some distance below the opening of the right superior vena cava. It is composed of fibres (Plate IV, fig. 21) in which the longitudinal fibrillae are limited to the periphery, the central parts of the fibres being very clear and staining very pale. In many of the cells of which the fibres consist, two nuclei, centrally situated and round in shape, can be seen. The fibres form intricate inter-crossings and interspersed between them there is a fair amount of connective tissue. For the most part the fibres are larger than the ordinary auricular myocardial fibres; smaller fibres are in a minority. The fibres are continuous with the adjacent ordinary cardiac muscle of the right auricle. They appear also to establish continuity with the sub-endocardial Purkinje fibres in the neighbourhood. No nerve cells are present in the mass itself, but small ganglia and nerve fibres are plentiful in the epicardial connective tissue in this region, and nerve fibres can be traced towards the mass but are not conspicuous in the mass itself. Two branches of the right coronary artery run longitudinally, one in front of and one behind

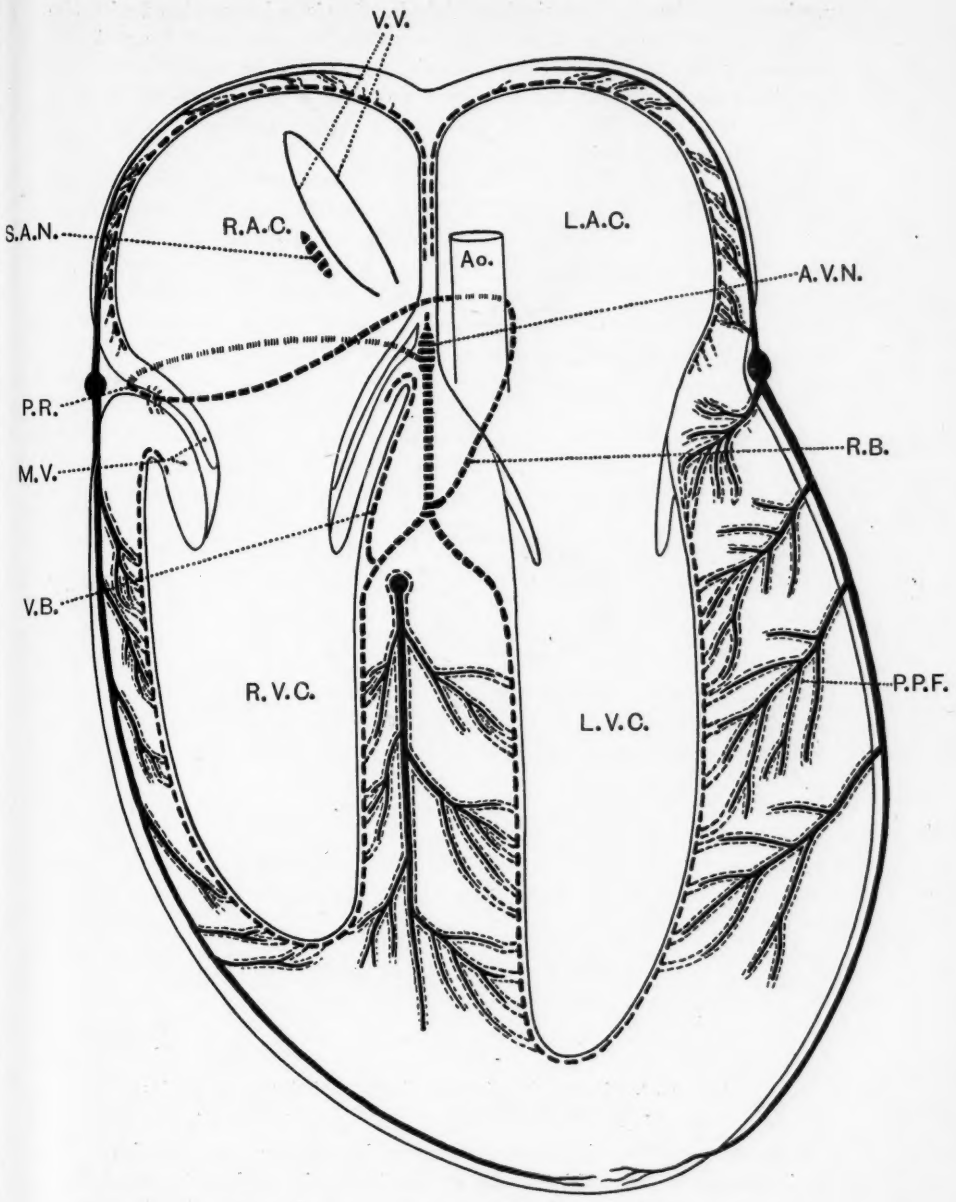
the mass, and an anastomosing vessel connecting these two arteries passes through the mass, an arterial arrangement very similar to that which occurs in the region of the sinu-auricular node in the mammalian heart. The above morphological data are evidence that the lightly staining ovoid mass in the base of the right venous valve is the avian sinu-auricular node. Confirmation will be sought by future experimental work.

DISCUSSION

The conducting system of the avian heart (text-figure 3) is seen from the present investigation to consist mainly of:

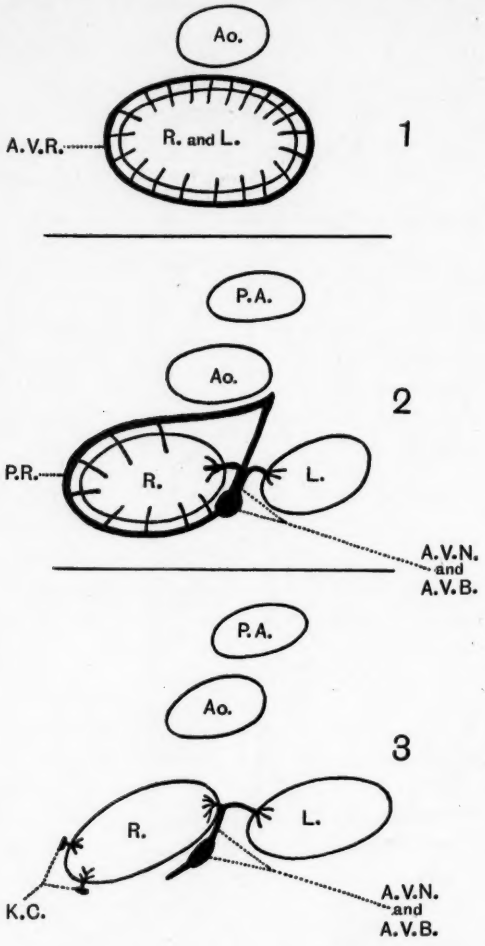
(*a*) sinu-auricular node, and auricular sub-endocardial and peri-arterial Purkinje ramifications; and

(*b*) auriculo-ventricular node, and right auriculo-ventricular ring of Purkinje fibres, both establishing connections between auricle and ventricle, the A.-V. node by means of the auriculo-ventricular bundle and its two limbs ending in the ventricular sub-endocardial and peri-arterial Purkinje ramifications, and the right auriculo-ventricular ring of Purkinje fibres by means of its connections with the auricular and ventricular myocardial components of the muscular valve. It is interesting and instructive to compare the special auriculo-ventricular connections of the bird's heart thus determined, with those of the mammalian heart on the one hand and with those of the fish and reptilian heart on the other (text-figure 4). In the fish and lower reptile heart a ring of specialised fibres (auriculo-ventricular ring), at the junction of auricle and ventricle, establishes continuity between these chambers of the heart in its entire circumference. In the mammalian heart, with the development of *membranous* auriculo-ventricular valves and auriculo-ventricular fibrous rings, the auriculo-ventricular ring of special tissue becomes reduced or narrowed, and the remaining connection between auricle and ventricle is represented by the auriculo-ventricular node, the auriculo-ventricular bundle and its two limbs being developed in association with the separation of the ventricles by a septum. (There is some evidence, however, that the A.-V. node is a derivative of the sinu-auricular, and not of the auriculo-ventricular ring, namely, that the right vagus and the right sympathetic are associated experimentally with the sinu-auricular node, and the left vagus and left sympathetic with the auriculo-ventricular node, both nodes being considered thus to be derivatives of the sinu-auricular ring.) It is possible that the accessory auriculo-ventricular connections described by Stanley Kent (17), and confirmed by Todd and van der Stricht (18 and 19), are persistent derivatives of the auriculo-ventricular ring. In the avian heart, the auriculo-ventricular node and the auriculo-ventricular bundle with its two limbs have been developed, and in addition the auriculo-ventricular ring to some extent retained. The avian auriculo-ventricular connections thus present an arrangement intermediate between those of the fish and reptile and those of the mammal. The



Text-fig. 3. Diagram summarising main topographical disposition of avian conducting system.

persistence of the special auriculo-ventricular ring is to be correlated with the muscular structure of the right auriculo-ventricular valve, and the auriculo-ventricular bundle and its divisions with the complete separation of the ventricles by a septum; the distribution of one limb to each ventricle is



Text-fig. 4. Diagram of specialised auriculo-ventricular connections in: 1. Fish and lower reptile; 2. Bird; 3. Mammal.

correlated with the simultaneous contraction of the two ventricles. The arrangement of the special tissue at the sinu-auricular junction also differs in the above species. In the fish heart there is a ring of special tissue (sinu-auricular ring) at the bases of the venous valves. In the reptilian (lizard)

heart specialised muscle at the sinu-auricular junction is limited to the base of the *left* venous valve, whereas in the mammalian heart it is limited to the upper part of the base of the right venous valve (upper part of sulcus terminalis). In the avian heart specialised muscle at the sinu-auricular junction is found in the base of the right venous valve, but relatively nearer the orifice of the inferior vena cava than in the mammalian heart. In addition to the above morphological variations in the conducting system of different species of animals, another factor controls the amount and extent of distribution of the Purkinje system, namely, the *rate of the heart beat.* The extensive distribution of the avian Purkinje system, both auricular and ventricular, sub-endocardial and peri-arterial, is correlated with the rapid heart rate in the bird. The patterns of the myocardial branches of the coronary arteries have been shown above to vary with the thickness of the cardiac wall, and in the case of the very thick free wall of the left ventricle, for instance, it is evident that the "tree-pattern" of distribution of the coronary arteries enables the peri-arterial Purkinje fibres to take a relatively short course through the thick myocardium. This accounts for the rapidity of arrival of the wave of excitation at a given point on the surface of the left ventricle wall in the bird's heart, as observed by Lewis (10).

The absence of a fibrous sheath about the avian auriculo-ventricular bundle and its divisions is similarly to be correlated with the rapidity of the heart rate, the necessity arising for early and widespread diffusion of the impulse from the auricle along the bundle to all parts of the ventricles, with consequent early and widespread continuity of the bundle and its divisions with the myocardium. The absence of a fibrous sheath about the bundle in the rapidly contracting avian heart also suggests the part played by the fibrous sheath about the mammalian A.-V. bundle. Lhamon (20) confirms the description of Tawara, who demonstrated that the fibrous sheath around the mammalian A.-V. bundle can be traced along the divisions of the bundle and the terminal Purkinje fasciculi to blend with the perimysium of the cardiac muscle where the Purkinje fibres blend with the myocardial fibres, thus isolating completely the conducting system from the neighbouring myocardium. This fibrous sheath can be injected with fluids like indian ink or prussian blue, and these injections demonstrate that the potential space between the sheath and the bundle is not continuous with the lymphatic system of the heart. Curran (21) described a "constant mucous bursa" about the mammalian A.-V. bundle, containing a fluid somewhat more viscid than lymph, and he attributed to the fibrous sheath a mechanical protective action in that it would diminish friction between the vigorously contracting myocardium and the *relatively* stationary bundle. If this were the function of the fibrous sheath, then, in the rapidly and vigorously contracting avian heart, where the A.-V. bundle is deeply embedded in the thick ventricular septum, a well-developed protective fibrous sheath would be expected to be present. The absence of an avian sheath, correlated as above stated with the rapidity

of the heart rate in the bird, suggests that the mammalian sheath, in the slower heart, is concerned with insulation of the bundle and its branches from the neighbouring myocardium. An analogy can be drawn between this action of the mammalian sheath and the insulating action of the neurilemma (Trotter(22)), which, for example, in the case of the motor nerve, insulates the axis cylinder right up to the region of continuity of conducting and contractile tissue.

The intimate relation between the aortic ends of the right auriculo-ventricular Purkinje ring and of the recurrent branch given off from the bifurcation of the main A.-V. bundle and the numerous small ganglia and nerve fibres at the base of the aorta, raises the question as to whether the Purkinje system plays any part at all on the *afferent* side of cardiac control. The recurrent branch of the main A.-V. bundle, given off at its bifurcation, and passing up through the ventricular septum just in front of the mitral valve, recalls the original description by His(23) of the left limb of the mammalian A.-V. bundle terminating in the base of the aortic (anterior) cusp of the mitral valve. Such an aberrant left branch has been described in abnormal human hearts (Morison(24)), and frequently in normal human hearts an abruptly ending process can be traced in this direction (Walmsley(25)).

SUMMARY AND CONCLUSIONS

1. The conducting system, of specialised structure, of the avian heart is described.

2. The special auriculo-ventricular and sinu-auricular connections in the bird's heart are compared with our present conception of those in the fish, reptilian and mammalian heart.

3. The extensive distribution of the avian Purkinje system is correlated with the rapidity of the heart rate.

4. The structure of the muscular right auriculo-ventricular valve is described, together with its influence upon the configuration of the conducting system.

5. The absence of a well-defined fibrous sheath about the avian bundle is noted, and its bearing upon the probable insulating action of the mammalian sheath is discussed. The absence of a sheath is also correlated with the rapidity of heart rate.

The above work was carried out in the Anatomical Department, University College, London. My thanks are due to my chiefs, Prof. G. Elliot Smith and Prof. J. P. Hill, for advice throughout the course of the work, also to Mr E. O. Lloyd, technical assistant, who prepared the microscopic sections, and to Mr F. Pittock, who prepared the microphotographs and lantern slides. The birds' hearts were kindly given me by Mr S. Zuckerman, Anatomist at the Gardens of the Zoological Society, London.

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DESCRIPTION OF PLATES I–IV

Plate I

Fig. 1. Oblique section through posterior part of junction of auricular and ventricular septum. Low power. Pigeon.
Fig. 2. Oblique section through upper part of ventricular septum. Low power. Black swan.
Fig. 3. Transverse section through upper quarter of ventricular septum. Low power. Black crake.
Fig. 4. Transverse section ventricular septum at level of bifurcation of A.-V. bundle. Low power. Black swan.
Fig. 5. Transverse section ventricular septum just below bifurcation of A.-V. bundle. Low power. Black swan.
Fig. 6. Transverse section ventricular septum below bifurcation of A.-V. bundle, at level where right limb of bundle approaches endocardium. Low power. Black swan.

Plate II

Fig. 7. Transverse section ventricular septum slightly above level of fig. 6. Low power. Black swan.
Fig. 8. Transverse section ventricular septum a little above level of fig. 7. Low power. Black swan.
Fig. 9. Transverse section ventricular septum at level where left limb of bundle approaches endocardium. Low power. Black swan.
Fig. 10. Transverse section ventricular septum above level of bifurcation of bundle. Low power. Black swan.
Fig. 11. Transverse section of aorta. Low power. Pigeon.
Fig. 12. Transverse section at junction of right auricle and ventricle. Low power. Pigeon.

PLATE III

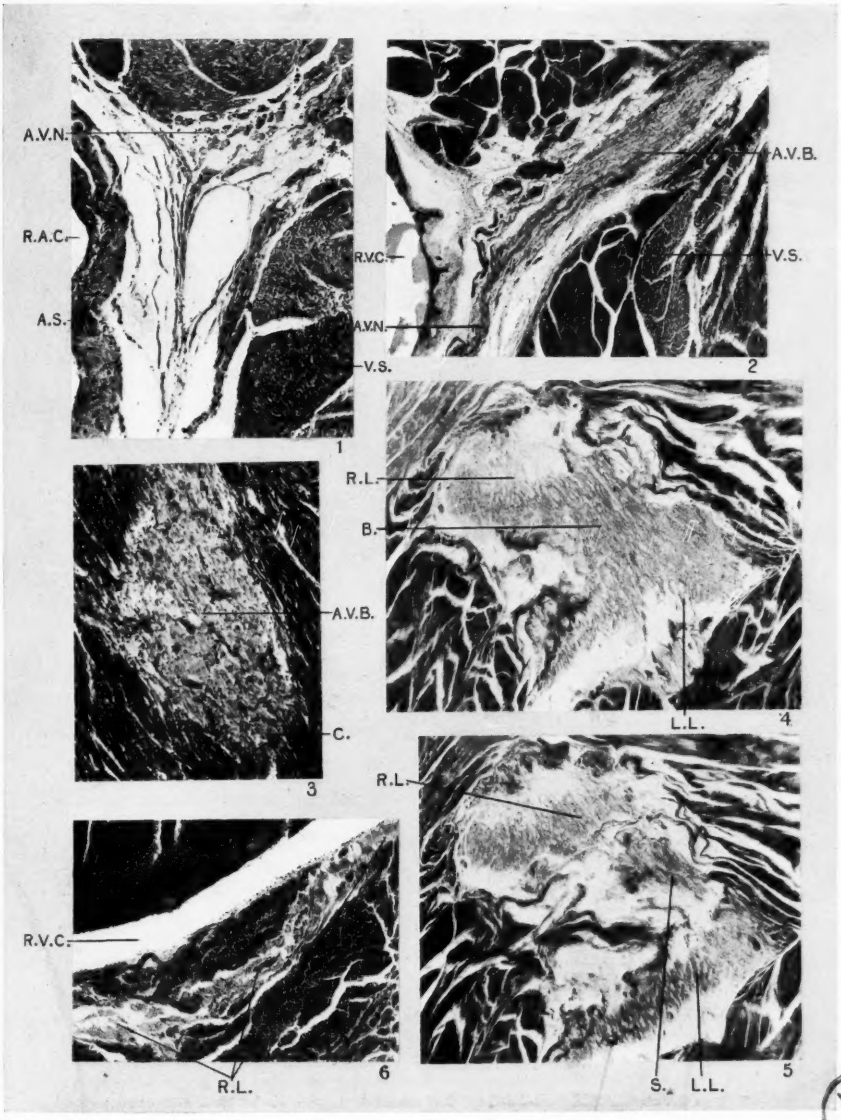
Fig. 13. Longitudinal section muscular valve. Low power. King penguin.
Fig. 14. Transverse section base of aorta. Low power. Pigeon.
Fig. 15. Transverse section muscular valve. Low power. Pigeon.
Fig. 16. Transverse section lower part left ventricle. Low power. Black swan.
Fig. 17. Transverse section lower part left ventricle. Low power. Black swan.
Fig. 18. Transverse section lower part left ventricle. Low power. Black swan.

PLATE IV

Fig. 19. Transverse section upper part left auricle. Low power. Black swan.
Fig. 20. Transverse section right auricle. Low power. Stork.
Fig. 21. High power view of lighter area in fig. 20. Stork.

ABBREVIATIONS USED IN PLATES AND TEXT-FIGURES

Ao.	Aorta.
A.S.	Auricular septum.
A.V.B.	Auriculo-ventricular bundle.
A.V.N.	Auriculo-ventricular node.
A.V.R.	Auriculo-ventricular ring of specialised muscle.
B.	Bifurcation of A.-V. bundle.
C.	Continuity of Purkinje and myocardial fibres.
C.S.	Coronary (auriculo-ventricular) sulcus.
En.	Endocardium.
Ep.	Epicardium.
K.C.	Accessory auriculo-ventricular connections of Stanley Kent.
L.	Left auriculo-ventricular orifice.
L.A.	Left auricle wall.
L.A.C.	Left auricle cavity.
L.C.A.	Left coronary artery.
L.L.	Left limb of A.-V. bundle.
L.V.	Left ventricle wall.
L.V.C.	Left ventricle cavity.
M.V.	Muscular right auriculo-ventricular valve.
P.A.	Pulmonary artery.
P.F.L.	Purkinje fibre cut longitudinally.
P.F.T.	Purkinje fibre cut transversely.
P.P.F.	Peri-arterial Purkinje fibres.
P.R.	Ring of Purkinje fibres about right auriculo-ventricular orifice.
R.	Right auriculo-ventricular orifice.
R.A.	Right auricle wall.
R.B.	Recurrent branch of A.-V. bundle.
R.A.C.	Right auricle cavity.
R.C.A.	Right coronary artery.
R.F.R.	Right auriculo-ventricular fibrous ring.
R. & L.	Common ventricular orifice.
R.L.	Right limb of A.-V. bundle.
R.V.	Right ventricle wall.
R.V.C.	Right ventricle cavity.
R.V.V.	Right venous valve.
S.	Spt[illegible] septal myocardium between right and left limbs of A.-V. bundle.
S.A.	Septa[illegible] artery.
S.A.N.	Sinu-auricular node.
S.P.F.	Sub-endocardial Purkinje fibres.
V.B.	Branch of right limb of A.-V. bundle to muscular valve.
V.S.	Ventricular septum.
V.V.	Venous valves (right and left).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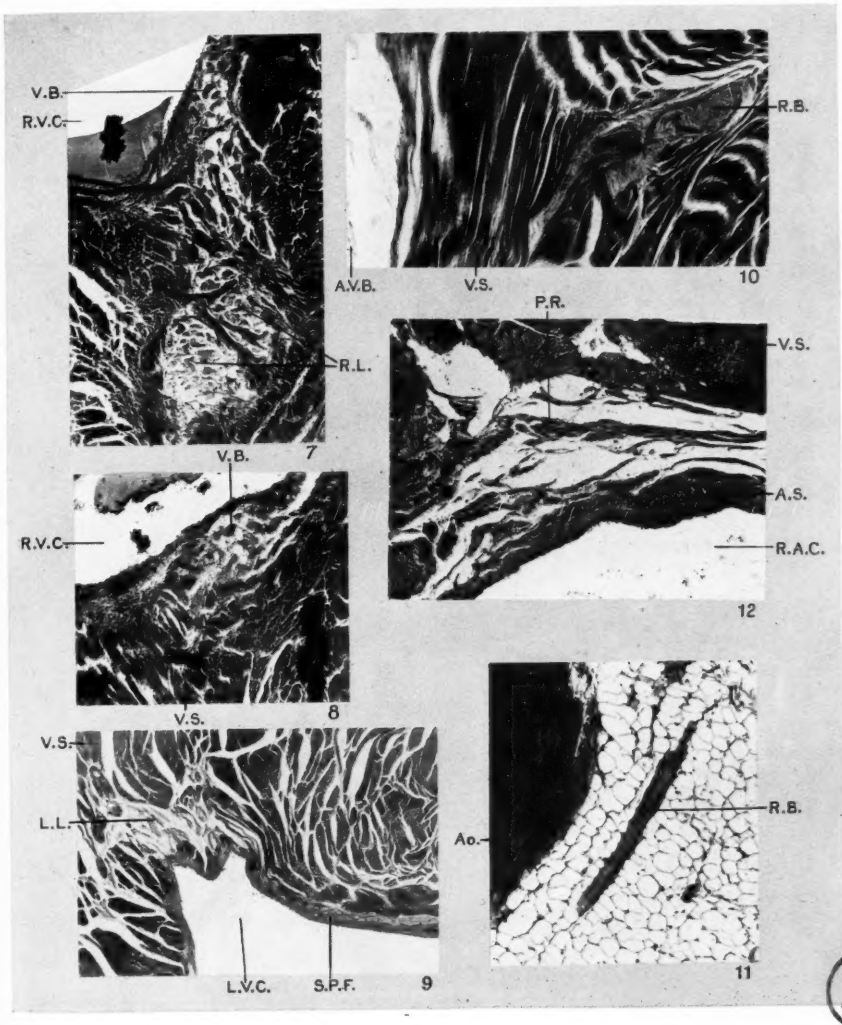
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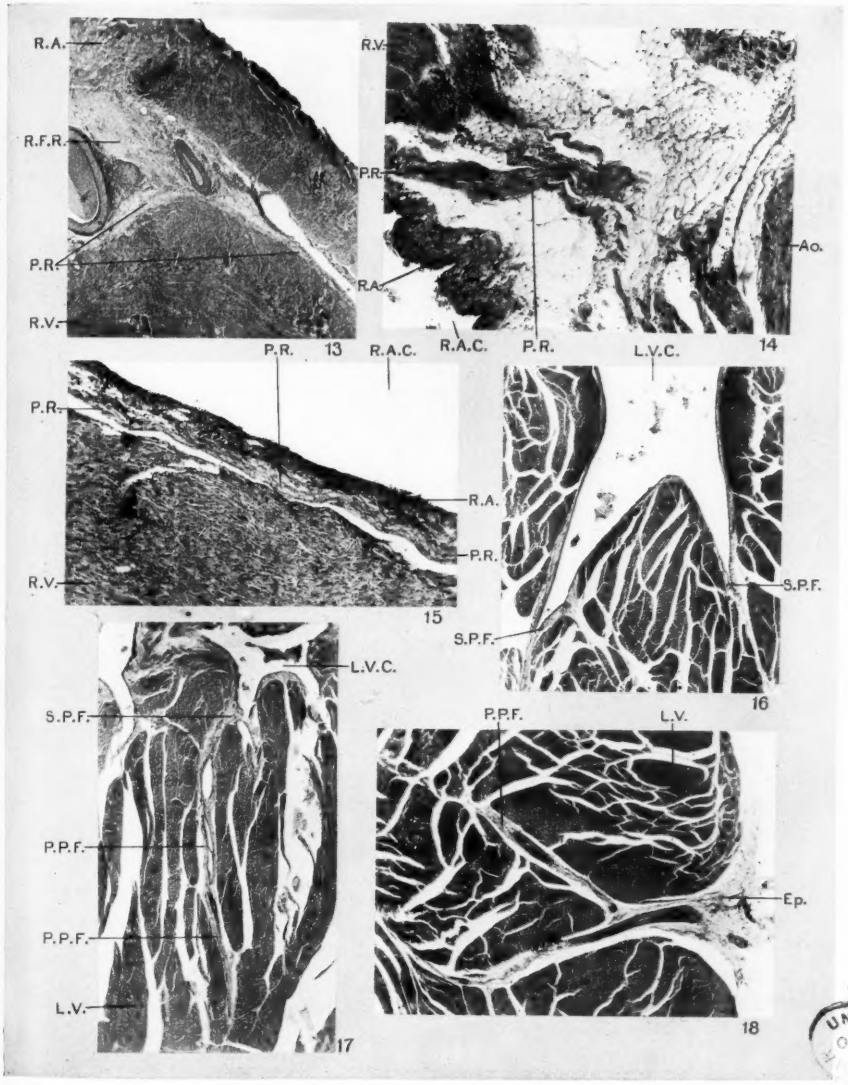
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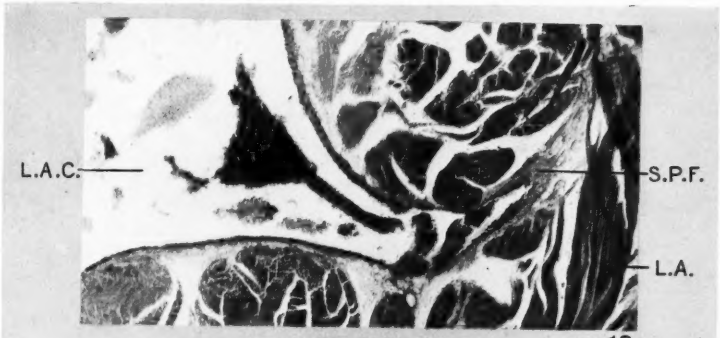

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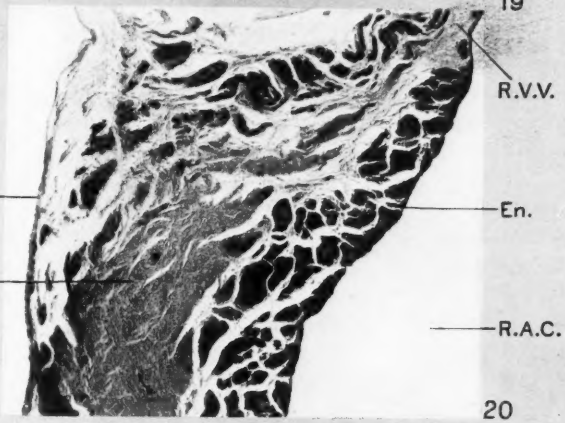

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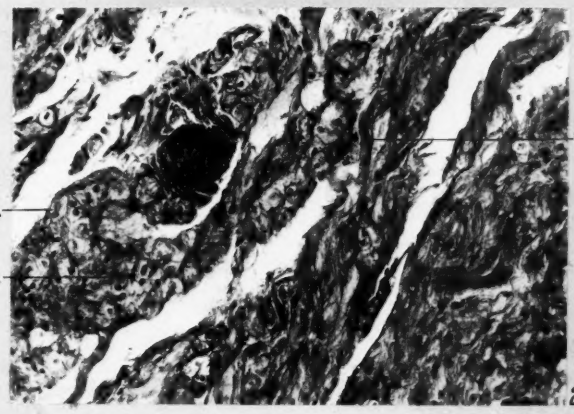

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UNIV. OF

LE *NEOPALLIUM* DES ÉQUIDÉS

ÉTUDE DU DÉVELOPPEMENT DE SES PLISSEMENTS

PAR R. ANTHONY,
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Chef de travaux à l'Université de Varsovie

LE *neopallium* des Ongulés est mal connu, en ce sens que l'on ne peut se dire, en dépit des recherches pourtant si précieuses de Holl[1], définitivement fixé sur la signification de ses plissements; en d'autres termes, on manque encore de certitude pour assimiler les plissements néopalléaux des Ongulés à ceux des Carnassiers par exemple dont la topographie cérébrale bien établie[2] peut en quelque sorte servir de point de départ.

La seule façon de reconnaître, dans un *neopallium* aussi compliqué et aussi variable dans ses détails que l'est celui des Ongulés, les plissements fondamentaux est de s'adresser à l'embryogénie; c'est ce que nous avons voulu faire tout d'abord pour les Périssodactyles qui sont, à cet égard, et pour plusieurs raisons, dignes d'un intérêt tout particulier: c'est notamment par la connaissance de leur *neopallium* que l'on doit parvenir à celle du *neopallium* plus complexe encore des Cétacés[3] que nous ne sommes pas, pour le moment, en état de bien comprendre[4].

Si nous débutons par l'étude des Equidés, c'est seulement parce qu'il est relativement facile de se procurer des embryons et des fœtus de cheval de tout âge.

Nous avons établi une série de 12 stades qui tous, sauf le stade 9 partiellement représenté par un fœtus d'Hémione, se rapportent au Cheval domestique.

STADE 1. No. 1913-380[5]. Longueur de la tête (du point le plus reculé de la région occipitale au point le plus avancé de la région nasale, sur la ligne médiane) = 47 mill.

STADE 2. No. 1927-296. ♀. Longueur de la tête = 69 mill. Longueur du fœtus (en projection) = 210 mill.

STADE 3. No. 1929-15. Longueur de la tête = 70 mill.

STADE 4. No. 1927-297. Longueur de la tête = 80 mill. Longueur du fœtus (en projection) = 220 mill.

[1] M. Holl, "Ueber die Insel des Ungulatengehirnes," *Archiv für Anatomie und Physiologie*, 1900.

[2] Voir R. Anthony, *Leçons sur le cerveau*, Paris: Doin, 1928.

[3] Voir R. Anthony, "Les affinités des Cétacés," *Annales de l'Institut océanographique*, 1926.

[4] Voir au sujet du *neopallium* des Cétacés R. Anthony, "Sur un cerveau de fœtus de Mégaptère," *C.R. Acad. des Sc.* 9 Nov. 1925.

[5] Numéro des réserves d'études du laboratoire d'Anatomie comparée du Museum national d'Histoire naturelle, Paris.

STADE 5. No. 1929-13. Longueur de la tête=104 mill.—No. 1927-295. Longueur de la tête=95 mill. Longueur du fœtus (en projection)=250 mill.

STADE 6. No. 1913-428. Longueur de la tête=117 mill. (6 mois environ).

STADE 7. No. 1927-294. Longueur de la tête=113 mill.

STADE 8. No. 1927-298. Longueur de la tête=95 mill. Longueur du fœtus (en projection)=290 mill.—No. 1927-299.

STADE 9. No. 1927-310. ♀. Longueur de la tête=146 mill. Longueur du fœtus (en projection)=360 mill.—No. 1917-5. ♂. Longueur de la tête=145 mill. Hémione [*Equus* (*Asinus*) *hemionus* Pall.].

STADE 10. No. 1927-575. Longueur de la tête=154 mill. Longueur du fœtus (en projection)=370 mill.

STADE 11. No. 1929-27. Longueur de la tête=180 mill.

STADE 12. No. 1912-98. Longueur du cerveau=80 mill. (la tête, incomplète, n'a pu être mesurée).

Ces stades ont été fixés d'après l'état du développement télencéphalique et non d'après la taille de l'animal (mieux exprimée par la longueur de la tête que par la longueur somatique totale qu'il est difficile de prendre exactement et toujours dans les mêmes conditions). La taille est, on le conçoit, susceptible de varier suivant les races; et, l'examen de ce tableau montre en effet qu'il arrive quelquefois que la tête se trouve être, à un certain stade, plus courte qu'à un stade précédent.

Bien que cet exposé soit essentiellement consacré au *neopallium*, nous avons cru devoir ajouter quelques indications sur le développement de la surface rhinencéphalique, d'ailleurs beaucoup moins intéressant que le développement des plissements néopalléaux.

STADE 1. A ce stade, le télencéphale diffère comme forme d'ensemble d'un télencéphale de Carnassier au même état de développement en ce que ses bords postérieur et antérieur sont, non pas obliques, mais à peu près perpendiculaires par rapport à l'axe longitudinal (voir Planche I, fig. I qu'il convient de comparer à la figure III).

Il présente seulement à la face externe (voir fig. 1, I et Planche I, fig. I) une légère indication de la rhinale (*r.a.* et *r.p.*) séparant le rhinencéphale du *neopallium*, et, de l'endorhinale (*er.*) séparant, dans le rhinencéphale, le *tractus olfactorius lateralis* du *tuberculum olfactorium* (*t.o.*). A ce stade, le *neopallium* est donc complètement lisse sur sa face externe. L'un de nous a montré que, chez les Carnassiers, la rhinale se développe d'abord en avant (rhinale antérieure)[1]. D'après l'examen du cerveau d'un animal un peu plus jeune que celui-ci, il semblerait que ce soit le contraire chez le Cheval. Nous verrons d'ailleurs qu'à l'âge adulte la rhinale postérieure est, chez le Cheval, beaucoup plus profonde que l'antérieure.

A ce moment, les rhinales forment par leur direction un angle de 111°; d'autre part, l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$ est égal à 82·8; à ces deux points de vue qui sont, comme nous le montrerons, étroitement liés, il est encore intéressant de comparer le télencéphale d'un Cheval à celui d'un Carnassier

[1] R. Anthony, *Leçons sur le cerveau*, pp. 270–1.

dans le même état de développement. Chez l'Ours nouveau-né par exemple dont le cerveau est, comme l'on sait, remarquablement peu développé (voir Planche I, figs. III et IV)[1] la valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$ est de 72·2, ce qui veut dire que le cerveau est plus allongé par rapport à sa hauteur que chez le cheval, et, les rhinales font un angle de 107°, par conséquent plus fermé que chez le Cheval. Nous verrons que, par la suite, chez les Equidés, l'angle des rhinales s'ouvre de plus en plus en même temps que la valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$ s'abaisse, le cerveau augmentant ainsi de longueur par rapport à sa hauteur.

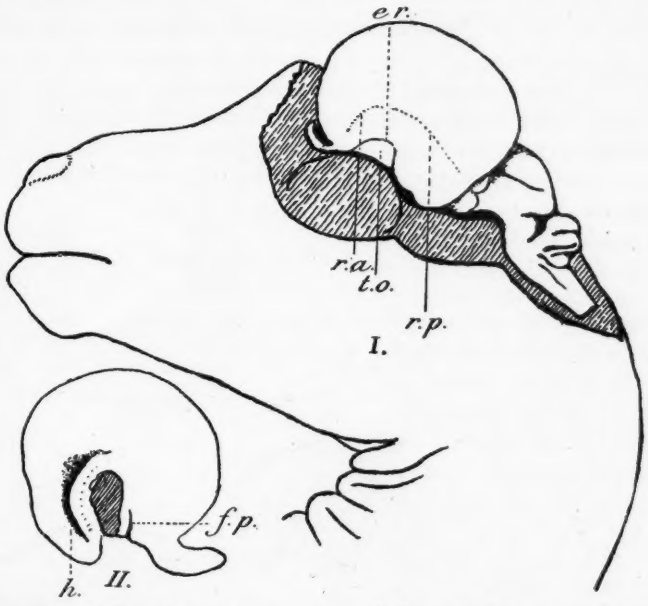


Fig. 1. Stade No. 1. I. Face latérale externe gauche. II. Face latérale interne gauche. G.N. ×2.

La forme très subsphérique du cerveau du cheval à ce stade est à noter d'une façon toute particulière, puisque l'on sait que le grand allongement du cerveau par rapport à sa largeur et à sa hauteur est, comme l'a rappelé Holl[2], un caractère fondamental des Périssodactyles, et, même, à part quelques exceptions très particulières, de tous les Ongulés adultes.

[1] Voir R. Anthony et F. Coupin, "Le Cerveau de l'Ours nouveau-né," *Album Societatis scientiarum Sevcenkianae Ucrainensium Leopoliensis ad solemnia sua decennalia quinta*, 1873–1923, Leopoli, A.D. 1925.—R. Anthony et J. Botez, "Le Développement du Cerveau de l'Ours," *Journ. of Anat.* 1925.

[2] M. Holl, *loco citato*.

Sur la face interne (voir fig. 1, II) on voit seulement la fissure hippocampienne (*h.*) déjà très profonde, mais qui n'est présente que dans la région retro-calleuse; dans le rhinencéphale, la *fissura prima* (*f.p.*) de His (*sulcus parolfactorius posterior*) est à ce stade très apparente. Le *gyrus dentatus* n'est pas morphologiquement séparé de la *fimbria* (absence de *fissura fimbrio-dentata*). De plus, comme sur la face externe, le *neopallium* est complètement lisse.

STADE 2.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 73{\cdot}8$. Angle des rhinales = 110°.

Ce stade est semblable au précédent avec cette seule différence très importante que la surface néopalléale située au-dessus de la région moyenne des rhinales (région de l'angle) présente une dépression assez apparente.

STADE 3.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 75{\cdot}3$. Angle des rhinales = 107°.

Sur la face externe du télencéphale (voir fig. 2, I et III), on distingue, en plus de la rhinale et de l'endorhinale (stade 1) ainsi que de la dépression située au-dessus de l'angle des rhinales (stade 2): 1°, sur le rhinencéphale, le sillon innominé (*a.*) qui sépare le *gyrus olfactorius lateralis* du *tractus* correspondant; 2°, sur le *neopallium*: d'une part, un assez profond sillon (*e.*) qui part un peu en arrière de l'angle des rhinales se dirigeant en avant et en haut; au delà du point où commence ce sillon, la scissure rhinale postérieure s'est légèrement approfondie, semblant comme se continuer avec lui. Ce sillon qui est en somme la limite supérieure de la dépression signalée au stade 2 ne peut être interprété que comme l'avait interprété Holl d'après l'étude du cerveau de l'adulte[1], c'est à dire comme une *ectosylvia*, car, entre lui et la rhinale, on ne voit exister aucun plissement. Cette

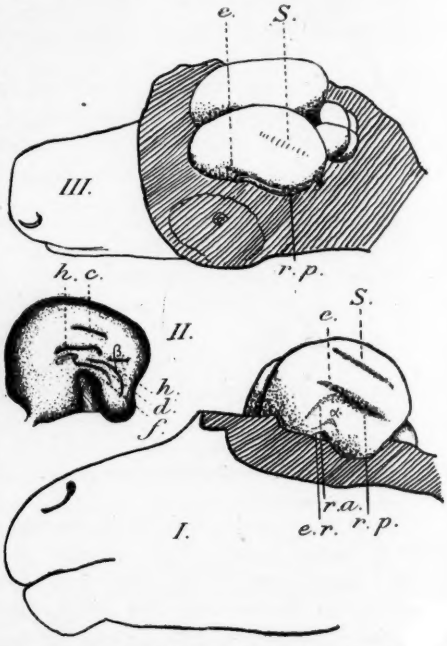


Fig. 2. Stade No. 3. I. Face latérale externe gr .e. G.N. II. Face latérale interne droite. G.N. III. Face supérieure, vue légèrement de 3/4. G.N.

[1] M. Holl, *loco citato*.

ectosylvia est courte et ne présente aucune flexion. Au-dessus d'elle et parallèlement à elle, est une dépression longitudinale obscure (*S.*) figurant la première ébauche de la *suprasylvia.*

La question qui se pose est celle de savoir laquelle des deux scissures *ectosylvia* ou *suprasylvia* se développe la première. Si l'on se reporte à la description du stade 2, c'est évidemment l'*ectosylvia*, la dépression signalée au-dessus de la région moyenne des rhinales en étant certainement, et comme nous venons de le dire, la première indication.

Sur la face interne (voir fig. 2, II et Planche I, fig. II) la *fissura hippocampi* (*h.*) se prolonge maintenant au-dessus du corps calleux présentant, à la hauteur du *splenium*, son interruption normale (*gyrus Andreae Retzii*).

La *fissura fimbrio-dentata* a commencé de s'indiquer, mais seulement dans sa région supérieure, ce qui revient à dire que la *fimbria* (*f.*) et le *gyrus dentatus* (*d.*) ne font que commencer à se séparer. La calcarine (*c.*) est indiquée par une dépression longitudinale située au niveau du *splenium* du corps calleux. Au-dessous, est une autre dépression également longitudinale (β.) qui ne répond pas en réalité à un véritable sillon, mais résulte de la présence et du contact en cet endroit du cerveau moyen.

STADE 4.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 83{\cdot}9$. Angle des rhinales = 126°.

Face externe (voir fig. 3): Les modifications à signaler sont, sur le *neopallium*: l'augmentation de profondeur de l'*ectosylvia* (*e.*) et de la *suprasylvia*

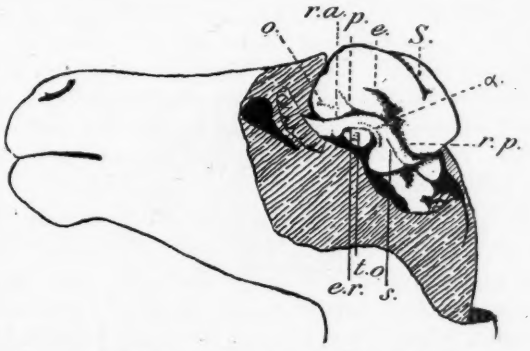


Fig. 3. Stade No. 4. Face latérale externe gauche. G.N.

(*S.*). La première (*e.*) s'est légèrement incurvée en raison de l'extension de la région située au-dessous d'elle et paraît dessiner un angle très ouvert en bas et en avant; sa lèvre supérieure s'est aussi développée considérablement dans sa région antérieure marquant ainsi le début de l'operculisation future. La seconde (*S.*) présente en arrière une courte bifurcation sur laquelle nous

aurons à revenir. En outre, la *presylvia* (*p.*) a pris naissance; on la voit se jeter dans la rhinale antérieure (*r.a.*) et, fait important, la dépression encore obscure qui lui correspond se continue, bien qu'étant en cet endroit particulièrement atténuée, avec celle de la *suprasylvia* (*S.*). Enfin, en avant de la *presylvia* (*p.*) est une ébauche d'orbitaire (*o.*).

Au rhinencéphale, on observe, sur le *lobus piriformis*, l'apparition du *sulcus sagittalis* (*s.*) qui entame légèrement le bord postérieur de l'hémisphère.

Face interne: On doit seulement noter l'accentuation de la calcarine.

Ce qui ressort de l'examen de ces quatre premiers stades, c'est:

1°, qu'au début le télencéphale est de forme subsphérique et que l'angle formé par les rhinales est relativement fermé, quoique plus ouvert que chez un Carnassier, comme l'Ours, au même stade de développement; ultérieurement, le télencéphale s'allongera par rapport à sa hauteur et ce processus s'annonce déjà; d'autre part, l'angle des rhinales s'ouvrira de plus en plus; déjà il commence à s'ouvrir;

2°, que le sillon d'operculisation est, chez les Equidés, comme chez l'*Ursus*, et d'une façon plus générale chez les Carnassiers arctoïdes qui sont les seuls Carnassiers fissipèdes[1] où une partie du territoire central est operculisé, l'*ectosylvia* et non la *suprasylvia* comme chez les Primates, donnée déjà acquise depuis Holl, d'où il s'ensuit que l'operculisation ne porte ici que sur le *gyrus arcuatus* I de Leuret;

3°, que l'*ectosylvia* se développe avant la *suprasylvia* comme chez les Carnassiers à territoire central partiellement operculisé (*Ursus* par exemple)[2]; il convient de remarquer que chez l'*Ursus*, on constate aussi, avant l'apparition de tout sillon sur la face externe du *neopallium*, notamment avant toute indication de la *suprasylvia*, comme au stade 2 chez le Cheval, au-dessus de l'angle des rhinales, une dépression obscure et qui correspond à la région qui s'operculisera plus tard. On comprend au surplus que, partout, la scissure d'operculisation, étant nécessairement particulièrement profonde, doive, quelle qu'elle soit, se développer plus tôt;

4°, que, dès le début de son apparition, l'*ectosylvia* est en arrière au contact de la rhinale postérieure;

5°, que la *suprasylvia* se développe d'abord en avant comme chez les Carnassiers (*Ursus* et Chat domestique par exemple[3]); nous verrons en effet que la *suprasylvia*, telle qu'elle se présente au stade 3, se poursuivra en arrière dans les stades ultérieurs;

6°, que l'*ectosylvia* et la *suprasylvia* sont beaucoup moins fortement arquées qu'elles le seraient chez un Carnassier au même état de développement.

[1] On sait que les Pinnipèdes qui sont d'ailleurs des Arctoïdes adaptés à la vie dans les eaux se comportent à cet égard comme les Fissipèdes arctoïdes.

[2] Voir R. Anthony et J. Botez, *loco citato*.

[3] Voir R. Anthony, *Leçons sur le cerveau*.

STADE 5. Ce stade est représenté par deux individus. L'un (No. 1929-13) présente seulement, sur la face externe (voir Planche I, fig. V), et comme acquisition nouvelle, l'indication des nombreux sillons secondaires qui existent chez l'adulte entre la *suprasylvia* (*S.*) et l'*ectosylvia* (*e.*). On voit par exemple sur la figure V de la Planche, au-dessus de la courbure de l'*ectosylvia* (*e.*), l'indication d'un sillon longitudinal légèrement arqué que Holl[1] désigne sous le nom de *suprainsularis*, et plus en avant celle du *diagonalis* du même auteur[2].

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 75{\cdot}8$. Angle des rhinales = 130°.

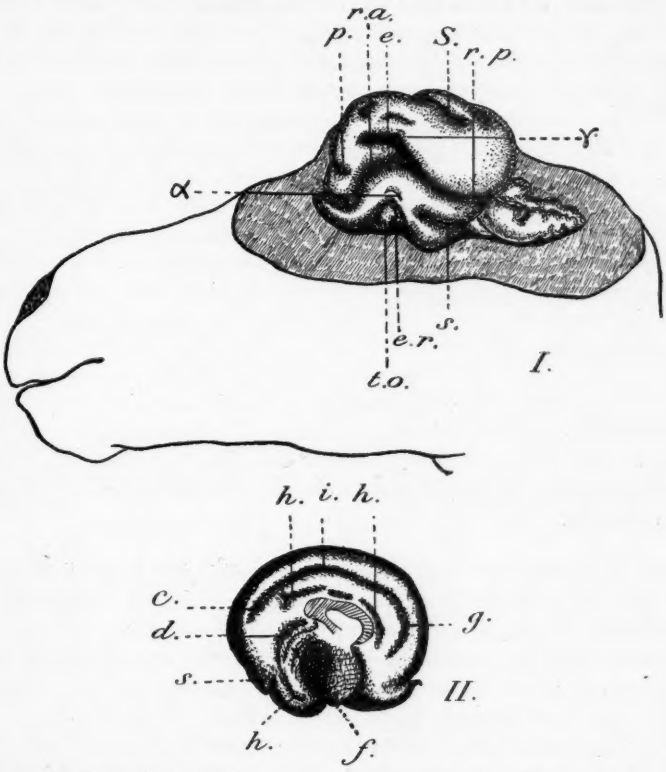


Fig. 4. Stade No. 5. I. Face latérale externe gauche (No. 1927-295). G.N.
II. Face latérale interne gauche (No. 1927-295). G.N.

L'autre individu (No. 1927-295) (voir fig. 4, I) présente, outre les indications du *suprainsularis* et du *diagonalis* de Holl, cette particularité que la *presylvia* (*p.*) s'atténue dans sa région postérieure, c'est à dire au moment où elle va entrer en contact avec la rhinale antérieure.

[1] M. Holl, *loco citato.* [2] M. Holl, *loco citato.*

Chez ces deux individus l'expansion de la lèvre supérieure de l'*ectosylvia* (*e.*) a sensiblement augmenté; on assiste en d'autres termes aux progrès de l'operculisation du *gyrus arcuatus* I de Leuret.

A ce stade, il n'existe encore aucun début de *pseudosylvia*. Mais, sur la lèvre operculisante de l'*ectosylvia*, on voit la première indication nette (γ.) de l'encoche très accusée et très étendue qui existe constamment chez l'adulte au niveau de l'angle des rhinales. Une très légère indication de cette encoche existait déjà d'ailleurs au stade 4 (voir fig. 3). L'encoche (γ.) que nous voyons se présenter chez les Ruminants sous l'aspect d'un sillon beaucoup plus long et plus important est l'ébauche d'un véritable complexe sylvien. Il est à noter que ce complexe développé au dépens du *gyrus arcuatus* I affecte une direction verticale et non pas oblique comme chez l'Ours et chez les Primates, ce qui est en rapport avec l'allongement et le surbaissement du cerveau.

Sur la face interne (voir fig. 4, II) il convient de noter, chez l'individu No. 1927-295, le développement du splénial avec ses deux segments postérieur et moyen, calcarine (*c.*) et intercalaire (*i.*) auxquels le *genualis* (*g.*) s'ajoute en avant, en continuité avec l'intercalaire (*i.*). Sur cette même face interne, on voit aussi la grande largeur du *gyrus Andreae Retzii* et le passage sur la face interne du rhinencéphale de l'extrémité postérieure du *sulcus sagittalis* (*s.*). Ce passage se traduit par la présence d'une encoche qui entame le bord postérieur de l'hémisphère beaucoup plus fortement et sur un beaucoup plus long trajet qu'au stade 4. Nous avons observé souvent, chez d'autres Mammifères, cette encoche qu'il est facile d'apercevoir au cours du développement, et, surtout, chez les formes à télencéphale peu compliqué; mais nous n'avions pu en saisir la signification exacte en raison de l'absence du *sulcus sagittalis* sur la face externe du lobe piriforme; nous croyons qu'il faut la rattacher, partout où elle se trouve, au *sulcus sagittalis* dont elle pourrait même être parfois la seule partie existante.

Stade 6. Ce stade (voir fig. 5) est surtout caractérisé: 1°, par l'allongement du *suprainsularis* de Holl; 2°, par le développement du latéral (*l.*) et de l'ectolatéral (*ecl.*); 3°, par l'allongement de l'extrémité de la *presylvia* (*p.*) qui arrive presque au contact de la *suprasylvia* (*S.*), sans cependant se confondre avec elle. Cet allongement se poursuivra dans les stades ultérieurs, de telle sorte qu'à l'âge adulte, chez le Cheval domestique[1], tout au moins, les deux sillons semblent le plus souvent en continuité, le pli de passage n'existant que dans la profondeur. Cette apparence de continuité est d'ailleurs en quelque sorte fondamentale, puisque nous avons vu (stade 3) la dépression originelle de la *presylvia* se continuer au début avec celle de la *suprasylvia* (*S.*); 4°, par l'allongement de la *suprasylvia* (*S.*) en arrière. Cette branche surajoutée de la *suprasylvia* et qui n'est autre chose, comme

[1] Chez un Zèbre de Grévy [*Equus* (*Hippotigris*) *Grevyi* M. Edw. No. 1913-58], nous avons constaté, à droite, la position presque superficielle du pli de passage qui est d'ailleurs très étroit; à gauche, ce pli de passage est un peu plus profond.

l'avait vu Holl[1], que la *postsylvia* qui en fait partie intégrante résulte de l'extension du rameau supérieur de la petite bifurcation signalée au stade 4 (voir fig. 3). Nous voyons nettement maintenant, et ceci est un fait sur lequel il faut particulièrement insister, que la *suprasylvia* n'est point ici arquée comme chez les Carnassiers, mais, au contraire, sensiblement rectiligne.

Fig. 5. Stade No. 6. Face supérieure. G.N.

Stade 7. Ce stade est surtout caractérisé sur la face externe (voir fig. 6, I et III), par l'apparition de l'entolatéral (III, *enl.*), et, du côté droit seulement, du crucial (III, *x.*), mais qui est uniquement visible sur la voûte et indépendant du reste du splénial; de l'examen de ce stade, il résulte que le crucial (*x.*) commence à se développer par sa région antérieure. A noter que les sillons situés entre la *suprasylvia* (*S.*) et l'*ectosylvia* (*e.*) montrent une plus grande complication; le sillon ζ. dont il sera question plus loin et qui, chez l'adulte, continue la direction de l'*ectosylvia* en restant séparé par un pli de passage superficiel ou profond est déjà bien indiqué.

La face interne (voir fig. 6, II) ne présente de particulier que la présence d'un sillon accessoire en arrière de la calcarine.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 68{\cdot}3$. Angle des rhinales = 113°.

Stade 8. Ce stade est représenté par deux individus, le No. 1927-299 étant un peu plus avancé que le No. 1927-298 duquel nous nous occuperons surtout. Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 67{\cdot}8$. Angle des rhinales = 124°. Pas plus qu'au stade précédent, il n'existe de connexions entre le crucial et l'intercalaire (voir fig. 7, II, *x.* et *i.*), mais le pli de passage qui les sépare est plus étroit. De plus, l'*ectosylvia* a poursuivi son développement en avant se continuant par l'amorce d'une courte branche verticale (δ.) surmontée d'une dépression (ζ.) qui tend à la continuer et qui représente un sillon toujours séparé de l'*ectosylvia* par un pli de passage superficiel ou profond (voir stade 7). La *presylvia* (*p.*) est, comme au stade 5, séparée de la rhinale antérieure (voir fig. 7, I et Planche I, fig. VI). Il faut aussi noter que le *diagonalis* et le *suprainsularis* de Holl ont accusé leur développement. La région operculisée est encore dépourvue de tout sillon; il n'y a notamment pas encore d'indication de *pseudosylvia*. La rhinale postérieure (*r.p.*) s'est approfondie. Mais ce qu'il convient surtout de signaler c'est l'aspect pris par la *suprasylvia* (*S.*) à sa région postérieure (voir fig. 7, I et Planche I, fig. VI): son extrémité postérieure

[1] M. Holl, *loco citato.*

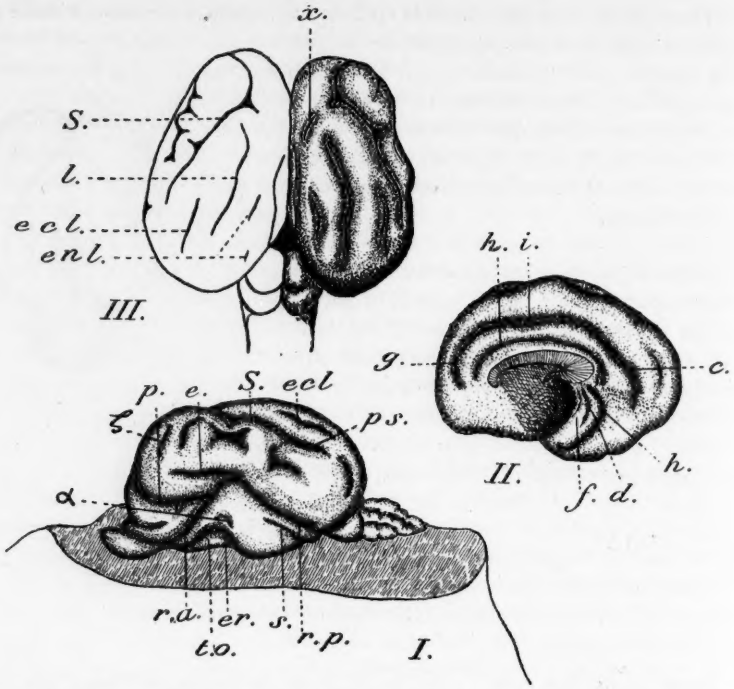


Fig. 6. Stade No. 7. I. Face latérale externe gauche. G.N. II. Face latérale interne droite. G.N. III. Face supérieure. G.N.

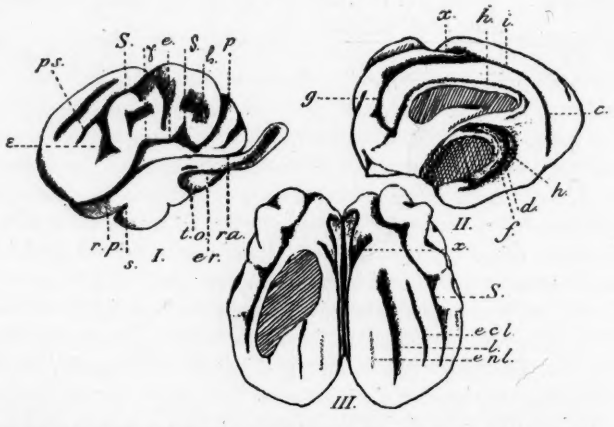


Fig. 7. Stade No. 8. I. Face latérale externe droite (No. 1927-298). G.N. II. Face latérale interne droite (No. 1927-298). G.N. III. Face supérieure (No. 1927-298). G.N.

se divise nettement en deux branches, l'une horizontale continuant sa direction qui est la *postsylvia* (*ps.*) dont nous avons déjà noté l'apparition au stade 6 (voir fig. 5), l'autre descendante (ζ.) dénommée par Holl[1] sillon oblique. L'examen des stades antérieurs nous permet de nous rendre compte de ce que la toute première apparition de ces deux branches est très précoce: au stade 4 (voir fig. 3), on les voit s'indiquer; aux stades 6 et 7 (voir figs. 5 et 6, I) on voit la *postsylvia* (*ps.*) déjà existante, alors que le sillon oblique de Holl ou n'a pas progressé (voir fig. 5) ou s'est développé indépendamment de la *suprasylvia*, comme cela existe peut-être chez l'individu No. 1927-294 (voir fig. 6, I). On pourrait évidemment être tenté de prendre ce que Holl appelle sillon oblique pour la *postsylvia*, la *suprasylvia* ayant ainsi dans sa totalité une forme arquée comparable à celle qu'elle affecte chez les Carnassiers. Mais, l'antériorité de développement de la branche horizontale sur la branche verticale est un argument puissant pour faire assimiler la première de préférence à la seconde à la *postsylvia*. La rectitude presque parfaite de la *suprasylvia* cadre d'ailleurs avec celle de l'*ectosylvia*, la grande ouverture de l'angle des rhinales et l'allongement antéro-postérieur du cerveau.

STADE 9. Hémione. C'est déjà presque l'apparence de l'adulte.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 60{\cdot}4$. Angle des rhinales = 121°.

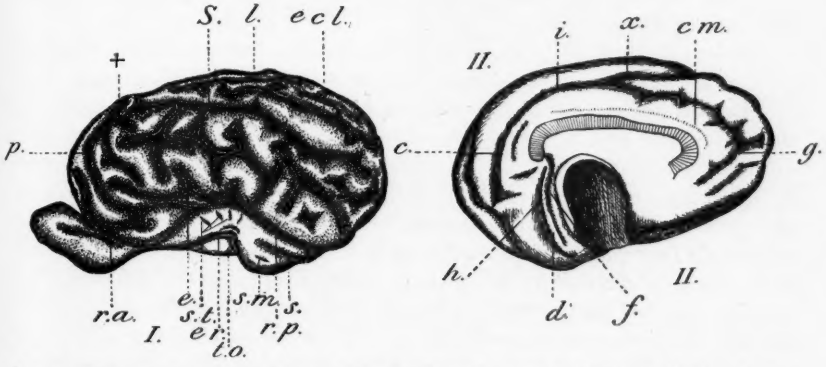


Fig. 8. Stade No. 9. I. Face latérale externe gauche (No. 1917-5, Hémione). G.N. II. Face latérale interne gauche (No. 1917-5, Hémione). G.N.

Sur la face externe (voir fig. 8, I), on voit apparaître, au rhinencéphale, un doublement du *sulcus sagittalis* (*sulcus sagittalis medialis—s.m.*) et les premiers *sulci transversi gyri olfactorii lateralis* (*s.t.*); au *neopallium*, la *presylvia* (*p.*) et la *suprasylvia* (*S.*) qui, comme il a été dit, se développent suivant une dépression continue sont ici séparées, de même qu'au stade 5, par un pli de

[1] M. Holl, *loco citato*.

passage superficiel (+) qui, dans la plupart des cas, se trouve, comme nous l'avons dit également, dans la profondeur, chez le Cheval adulte. La *presylvia* (*p.*) rejoint ici la rhinale antérieure (*r.a.*) et, le crucial (voir fig. 8, II, *x.*) qui semble rejoindre l'intercalaire (*i.*) en est, en réalité, séparé par un pli de passage très étroit et qu'on ne peut voir qu'en écartant les bords des circonvolutions. Le coronal (*c.*), très court, fait son apparition et semble en continuité avec la *presylvia* (*p.*) paraissant aussi rejoindre le crucial (*x.*)[1].

C'est ici qu'on voit la première ébauche de la *pseudosylvia*, un peu en arrière de l'angle des rhinales, et qui est représentée par un court sillon très peu marqué, oblique d'arrière en avant et de haut en bas. Cette ébauche commençant au sillon limite de la région operculisée (*ectosylvia*) est placée sur le plan en quelque sorte horizontal de cette région et n'atteint pas la rhinale, de telle sorte qu'on ne peut la voir qu'en soulevant la lèvre operculisante de l'*ectosylvia*.

La rhinale postérieure (*r.p.*) s'est encore approfondie, mais on ne voit point encore les sillons radiés qui garnissent, chez l'adulte, sa lèvre inférieure; il est facile de suivre la continuité entre la rhinale antérieure qui est sensiblement superficielle et le fond de la rhinale postérieure; à peu près au niveau de l'angle des rhinales, la scissure s'écarte de la surface pour aller rejoindre le fond de la cavité (*r.p.* sur la fig. VIII de la Planche).

A la face interne (voir fig. 8, II), on ne voit plus de trace de fissure hippocampienne dans la région supracalleuse. La *fissura fimbrio-dentata* est développée sur toute sa longueur (entre *d.* et *f.*).

Au *neopallium*, il faut noter l'apparition du *sulcus calloso-marginalis* (*c.m.*).

A ce même stade, se rattache le No. 1927-310 un peu moins avancé.

Chez cet animal, sur la face externe du rhinencéphale (voir fig. 9, I), les *sulci transversi gyri olfactorii lateralis* n'existent pas encore. Sur la face externe du *neopallium*, le pli de passage supra-présylvien est dans la profondeur. La *pseudosylvia* n'est pas visible, comme chez l'animal précédent, sauf peut-être à gauche où elle se présente sous l'aspect d'une large dépression partant de l'*ectosylvia* mais n'atteignant pas la rhinale. Par contre, en avant de la place qu'elle doit occuper, et, en avant de l'angle des rhinales, s'est formé un petit sillon un peu plus long et plus marqué à droite qu'à gauche; ce sillon dirigé d'avant en arrière et de haut en bas est celui que nous avons marqué du chiffre 2 dans notre figure 9 (I) de même que dans notre figure 17. Le crucial (voir fig. 9, III, *x.*) est séparé de l'intercalaire (*i.*) par un étroit et profond pli de passage. Le coronal (voir fig. 9, III, *c.*) n'est bien représenté qu'à gauche et se montre sous l'aspect d'une courte bifurcation antérieure du crucial (*x.*). Les plis radiaires de la lèvre inférieure de la rhinale postérieure n'ont pas encore commencé à apparaître.

Sur la face interne (voir fig. 9, II), il a persisté un vestige en deux segments de *fissura hippocampi* (*h.*) dans la région supracalleuse, et la *fissura fimbrio-*

[1] L'état de la pièce ne permet pas d'étudier avec plus de précision les rapports du coronal avec la *presylvia* et le crucial.

dentata ne descend pas jusqu'à l'extrémité du crochet de l'hippocampe; le *calloso-marginalis* est également en deux segments, l'un antérieur, l'autre postérieur.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 62{\cdot}5$. Angle des rhinales = 120°.

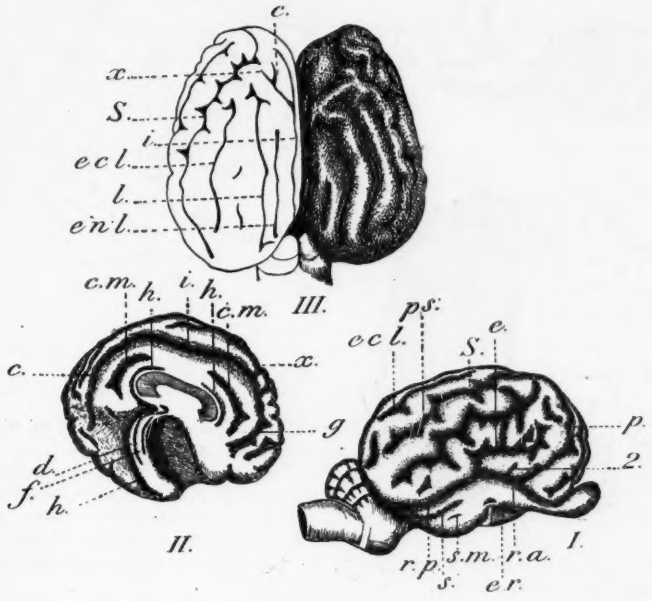


Fig. 9. Stade No. 9. I. Face latérale externe droite (No. 1927-310). G.N. II. Face latérale interne gauche (No. 1927-310). G.N. III. Face supérieure (No. 1927-310). G.N. C'est par un simple effet de raccourci que dans cette dernière figure le crucial (*x.*) semble en continuité avec l'intercalaire (*i.*).

STADE 10.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 65{\cdot}5$. Angle des rhinales = 127°.

Au rhinencéphale, on voit, pour la première fois, le *gyrus dentatus* (*d.*) prendre son aspect godronné caractéristique (voir fig. 10, II), le *gyrus ambiens* se compliquer, et le *gyrus lunaris* s'individualiser.

Les plis radiaires de la lèvre inférieure de la rhinale postérieure commencent à apparaître. Le rattachement de cette région operculisée au rhinencéphale et son interprétation comme lèvre inférieure de la rhinale postérieure peut s'appuyer sur l'examen histologique; bornons nous à constater (voir fig. 11) que les cellules corticales sont en effet beaucoup plus nombreuses à la lèvre supérieure de cette scissure qu'à sa lèvre inférieure. Le coronal (voir fig. 10, III, *c.*) est superficiellement relié au crucial (*x.*).

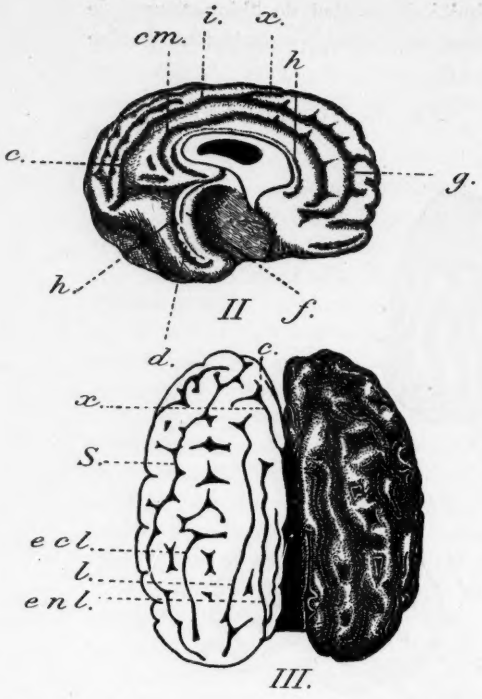


Fig. 10. Stade No. 10. II. Face latérale interne gauche. G.N. III. Face supérieure. G.N.

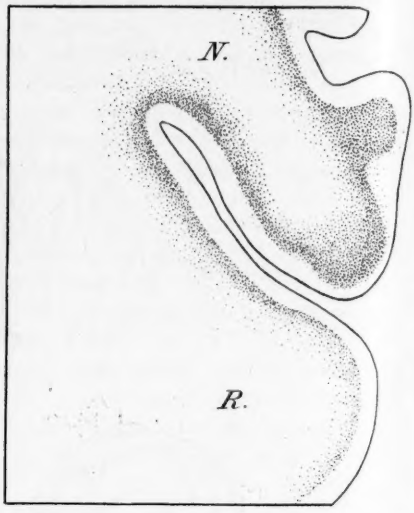


Fig. 11. Coupe coronale de la rhinale postérieure chez le No. 1927-575 (stade 10) montrant la constitution néopalléale du cortex de la lèvre supérieure, et la constitution rhinencéphalique du cortex de la lèvre inférieure de cette scissure; à la lèvre supérieure, les cellules corticales sont beaucoup plus nombreuses qu'à la lèvre inférieure.

STADE 11.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 61{\cdot}4$. Angle des rhinales = 122°

(voir fig. 12).

L'aspect de l'adulte commence à s'établir (voir fig. 12). A noter qu'à ce stade et sur cet individu, il n'existe plus de vestiges de *fissura hippocampi* dans la région supracalleuse; d'autre part les plissements de la lèvre inférieure de la rhinale postérieure sont plus développés. Remarquons aussi que le sillon (ζ.) est ici largement séparé de l'extrémité de l'*ectosylvia* (*e.*).

STADE 12.

Valeur de l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}} = 55{\cdot}7$. Angle des rhinales = 121°.

Ce stade peut être considéré comme semblable à un adulte. Nous nous bornerons à le figurer (voir fig. 14).

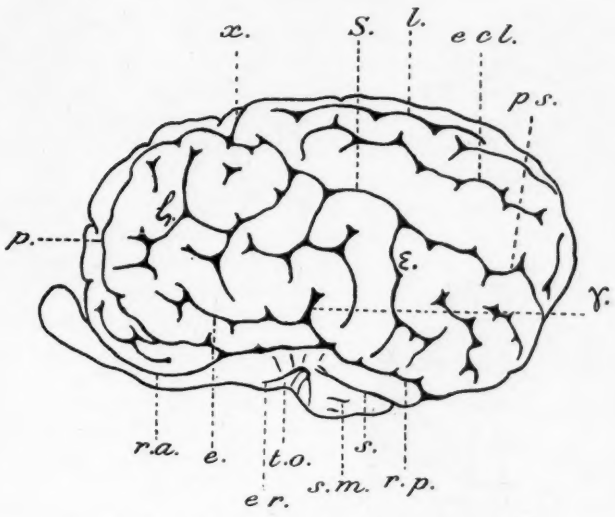


Fig. 12. Stade No. 11. Face latérale externe gauche. G.N.

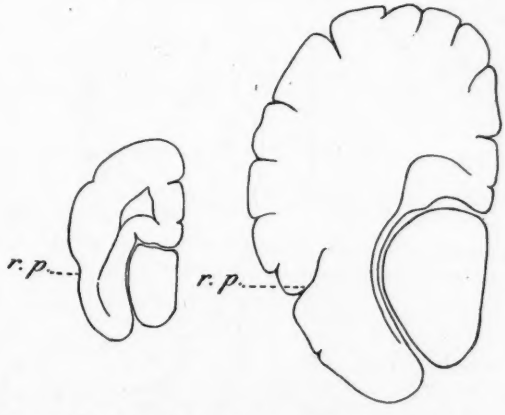


Fig. 13. Coupe transversale du télencéphale des Nos. 1927-295 (stade 5) à gauche, et 1929-27 (stade 11) à droite; pour montrer l'augmentation progressive de profondeur de la rhinale postérieure. G.N.

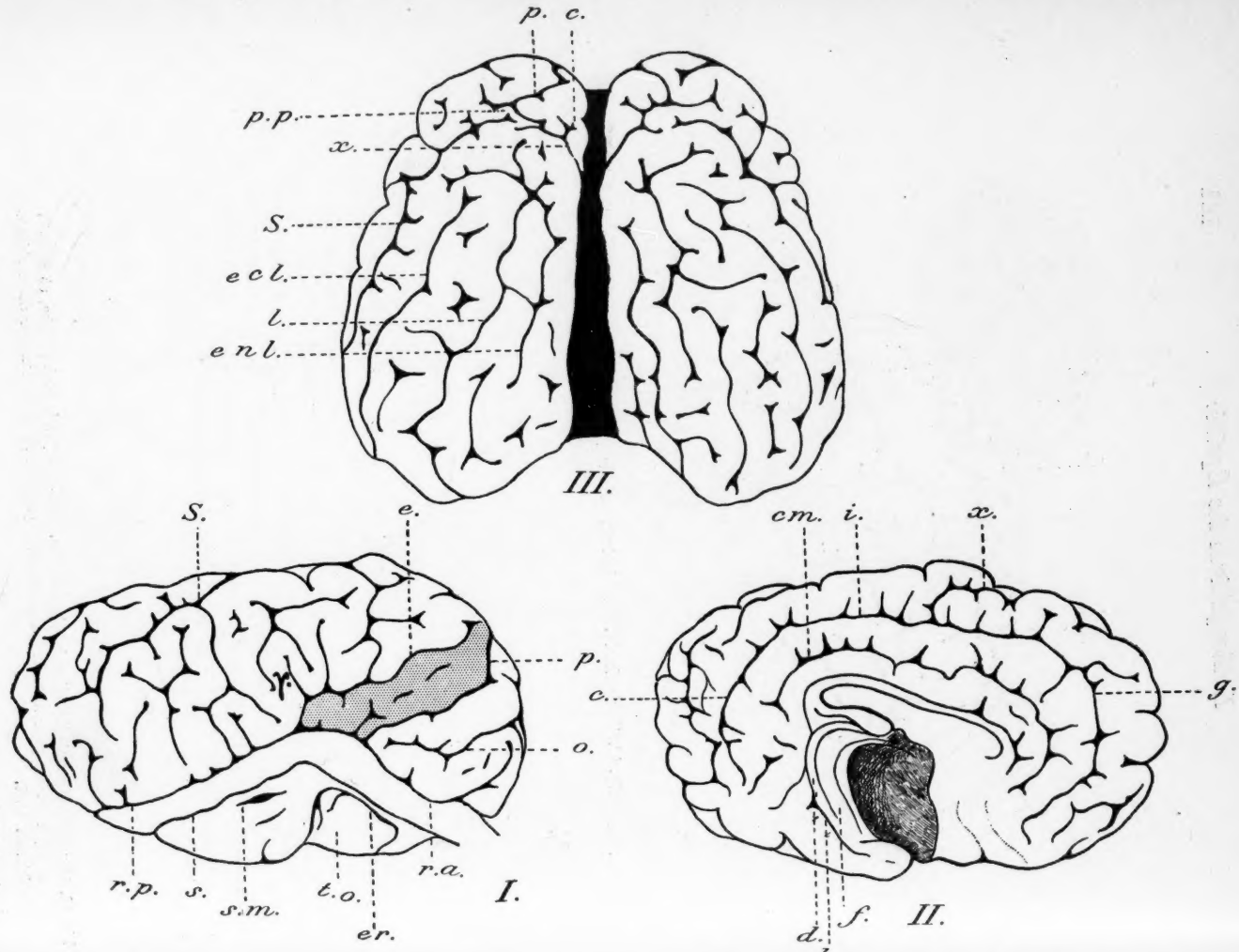


Fig. 14. Stade No. 12. I. Face latérale externe droite. G.N. Le *gyrus reuniens* et la partie visible du *gyrus arcuatus* I de Leuret (bras antérieur)

CARACTÈRES FONDAMENTAUX DU *NEOPALLIUM* DES ÉQUIDÉS ADULTES

Holl[1] a noté que le *neopallium* du Cheval domestique est extrêmement variable; les différences n'altèrent cependant jamais le type fondamental de la famille qui est très homogène. Ne voulant, ni ne pouvant, entrer ici dans le détail des variations spécifiques, raciales ou individuelles, nous avons cru devoir nous en tenir à la description d'un seul type d'Equidé; et nous avons choisi un cerveau de Zèbre de Grévy [*Equus* (*Hippotigris*) *Grevyi* M. Edw. No. 1913-58] pensant y trouver moins de complications et une forme plus primitive que dans celui du Cheval domestique. Nous nous réservons d'ailleurs d'étudier plus tard et avec tous les détails que la question comporte les différences qui séparent les uns des autres les divers Equidés au point de vue de la morphologie néopalléale.

Chez le Zèbre de Grévy que nous avons examiné l'indice $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$ est égal à 53 et l'angle des rhinales mesure 138°. Ces deux quantités sont chez un Cheval domestique pris au hasard (No. 1925-38) respectivement 55 et 128°.

On voit d'après le tableau ci-dessous, et aussi d'après le graphique qui l'accompagne, qu'au cours du développement l'indice

$$\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$$

diminue chez le Cheval, ce qui veut dire que le télencéphale s'allonge par rapport à sa hauteur, en même temps que l'angle des rhinales s'ouvre de plus en plus. Il est certain que les autres Equidés se comportent à cet

	$\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$	Angle des rhinales
Stade No. 1	82·8	111°
Stade No. 2	73·8	110°
Stade No. 3	75·3	107°
Stade No. 4	83·9	126°
Stade No. 5	75·8	130°
Stade No. 7	68·3	113°
Stade No. 8	67·8	124°
Stade No. 9	62·5	120°
Stade No. 10	65·5	127°
Stade No. 11	61·4	122°
Stade No. 12	55·7	121°
Cheval adulte	55	128°

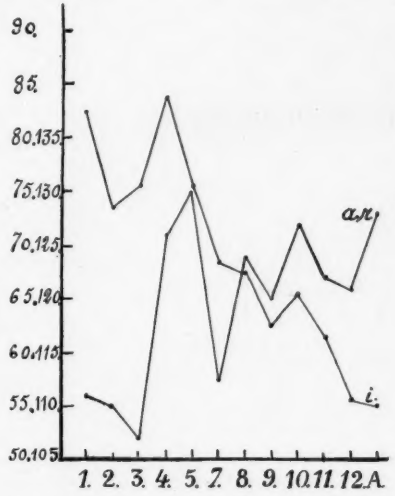


Fig. 15. Graphique pour montrer l'allongement progressif du cerveau par rapport à sa hauteur, diminution de valeur de l'indice (*i.*) $\frac{\text{Haut. tél.} \times 100}{\text{Long. tél.}}$, et l'ouverture progressive de l'angle des rhinales (*a.r.*), au cours du développement. La première colonne de chiffres verticaux indique la valeur de l'indice, la seconde celle de l'angle des rhinales.

[1] M. Holl, *loco citato*.

Fig. 14. Stade No. 12. I. Face latérale externe droite. G.N. Le *gyrus arcuatus* I de Lauret (bras antérieur) et la partie visible du *gyrus arcuatus* II, gyrus limitans antérieur.

égard exactement comme le Cheval. De plus, ces deux caractères, allongement par rapport à la hauteur et grande ouverture de l'angle des rhinales sont en quelque sorte essentiels au cerveau à la fois des Périssodactyles et des Artiodactyles. Holl[1] avait déjà noté d'ailleurs le premier de ces deux caractères qui différencie essentiellement, au moins dans la plupart des cas, le cerveau des Ongulés de celui des Carnassiers chez lesquels l'axe vertical est plus développé par rapport à l'axe longitudinal.

Quand on examine un cerveau d'Equidé par sa face latérale externe, on se rend compte immédiatement de ce que la rhinale postérieure est beaucoup plus profonde que l'antérieure; sa lèvre inférieure constitue, comme nous l'avons vu, une vaste région operculisée garnie de plis radiaires que l'examen microscopique montre bien dépendre du rhinencéphale (voir fig. 11). Holl[1], d'ailleurs, avait, par ses recherches sur l'adulte, déjà été amené à cette interprétation que les données embryologiques corroborent. De la rhinale postérieure on voit partir un peu en arrière de l'angle de flexion un très profond sillon oblique de bas en haut et d'arrière en avant présentant, après un court trajet, un angle très obtus ouvert en avant et en bas; ce sillon est ainsi que l'avait encore interprété Holl[1] l'*ectosylvia* qui présente en son point de coudure une bifurcation (γ.) dirigée de bas en haut et d'avant en arrière dont nous avons noté l'apparition précoce (stade 4) et qui représente un court complexe sylvien[2]. La lèvre supérieure de l'*ectosylvia* qui est très développée recouvre une région que nous étudierons tout à l'heure.

Dans la rhinale antérieure, en avant de l'angle des rhinales, se jette un autre sillon à peu près parallèle au premier; c'est la *presylvia*, interprétation encore en accord avec celle de Holl[1]. Pour se rendre compte de la certitude de l'identité de cette scissure avec la *presylvia* des Carnassiers et des Primates par exemple, il suffit de constater les rapports qu'elle affecte avec le *claustrum*[3] (voir Planche I, fig. VII).

Enfin, tout à fait en avant, au point où le bulbe olfactif s'individualise, se jettent, dans la rhinale antérieure, deux petits sillons qui sont les olfactifs ainsi qu'il ressort nettement de leurs rapports avec le bulbe.

Entre la *presylvia* et les olfactifs est un sillon représentant l'axe de la circonvolution arquée placée en cet endroit. Nous croyons pouvoir l'appeler orbitaire et l'assimiler à l'orbitaire des Primates par exemple. Holl[1] l'appelle *supraolfactorius* et pense devoir en faire une branche de la *presylvia* qui, chez le Cheval domestique, en reste quelquefois indépendante; cette conception nous paraît en contradiction avec la définition que l'un de nous a donnée de la *presylvia* et qui résulte de ses rapports, constatables ici comme chez les Carnassiers et les Primates, avec le *claustrum*[3].

La *suprasylvia* est un long sillon longitudinal dont l'extrémité antérieure n'est séparée de celle de la *presylvia* que par un pli de passage étroit le plus

[1] M. Holl, *loco citato*.

[2] Un complexe sylvien analogue existe chez les Ruminants, mais il est plus allongé.

[3] Voir sur les rapports de la *presylvia* et du *claustrum*: R. Anthony, *Leçons sur le cerveau*, 1928.

souvent profond. En arrière, la *suprasylvia* se divise en deux branches dont l'une (ϵ.), verticale, n'en fait point à la vérité partie, c'est le sillon oblique de Holl, et l'autre continuant sa direction est la *postsylvia*, partie intégrante de la *suprasylvia*. Il est à remarquer que la *suprasylvia* envisagée dans son ensemble (*suprasylvia* et *postsylvia*) n'est pour ainsi dire pas arquée alors que, chez les Carnassiers, elle l'est très fortement. Cette disposition qui est en rapport avec l'allongement du télencéphale est également marquée dans l'*ectosylvia*, ainsi qu'on peut mieux s'en rendre compte en réséquant la lèvre operculisante de cette scissure.

L'espace superficiel situé entre la *presylvia* et l'*ectosylvia* est le *gyrus reuniens* pour sa partie supérieure, la partie inférieure de cet espace représentant évidemment la région la plus antérieure du bras antérieur du *gyrus arcuatus* I de Leuret (voir fig. 14, I où l'espace en question est indiqué en grisé).

En parcourant la lèvre postérieure de la *presylvia*, il est facile de suivre le *gyrus reuniens* jusqu'au territoire périphérique, c'est à dire jusqu'au pli de passage tantôt superficiel tantôt profond qui sépare l'extrémité de la *presylvia* de celle de la *suprasylvia*, réalisant ainsi les connexions entre le territoire central et le territoire périphérique. Pour parvenir à ce dernier le *gyrus reuniens* traverse un autre défilé également très étroit entre l'extrémité de la *presylvia* et celle du sillon vertical (ζ.) qui continue la direction de l'*ectosylvia* (voir fig. 16, flèche), en étant cependant séparé, comme nous l'avons dit, par un pli de passage superficiel (voir fig. 12) ou profond.

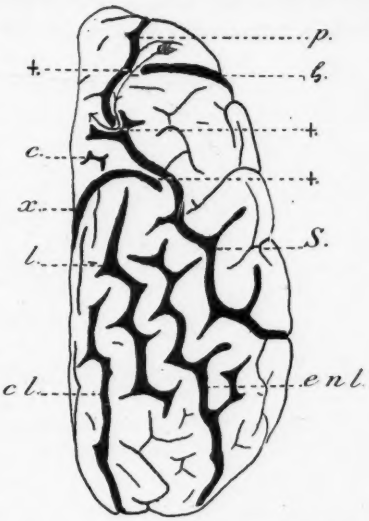


Fig. 16. Zèbre de Grévy No. 1913-58, demi-schématique. Face supérieure de l'hémisphère droit. 3/4 de G.N. Les sillons fondamentaux (*presylvia—ectosylvia—suprasylvia*—crucial—coronal—latéral—ectolatéral et entolatéral) et le sillon ζ. sont indiqués par de très gros traits, les autres par des traits beaucoup plus minces. Les plis de passage entre le crucial et la *suprasylvia*, entre la *suprasylvia* et la *presylvia*, entre le sillon ζ. et la *presylvia* qui sont en réalité profonds ont été reportés à la surface. La flèche contournée indique le trajet suivi par le *gyrus reuniens* du territoire central au territoire périphérique.

Au-dessus de la *suprasylvia*, sont l'ectolatéral, le latéral et l'entolatéral dont nous avons noté le moment d'apparition. Il est à remarquer que le crucial est assez peu développé et qu'il est indépendant de l'intercalaire avec lequel le *genualis* est au contraire en continuité; le *gyrus* sigmoïde est particulièrement étroit (voir fig. 16), ce qui tient au rapprochement du crucial et de la *suprasylvia*. Le coronal est aussi très peu développé; la place qu'il

a à occuper est d'ailleurs extrêmement restreinte (voir fig. 16); superficiellement, il semble le plus souvent relié au crucial et à la *presylvia*.

Pour étudier la région operculisée, il convient de réséquer tout à la fois la lèvre supérieure de l'*ectosylvia* et la lèvre supérieure de la rhinale postérieure en continuation l'une avec l'autre, ainsi que nous l'avons fait dans la figure schématique 17 et dans la figure VIII de la Planche.

On voit alors apparaître une vaste région que nous allons essayer d'expliquer (voir fig. 17). Suivons d'abord, dans sa profondeur, le sillon d'operculisation depuis *A* jusqu'à *B*. Nous voyons qu'il est divisé en deux parties au niveau d'un certain point *C* qui est celui où il est rejoint par le prolongement *EC*, parfois interrompu, de la rhinale antérieure *DE*. La partie *AC* est l'*ectosylvia*, la partie *CB* dépend de la rhinale postérieure dont elle constitue le segment postérieur, son segment antérieur étant constitué par *EC*. La rhinale postérieure apparente à la surface est *EF*. L'examen de la figure 17 montre que

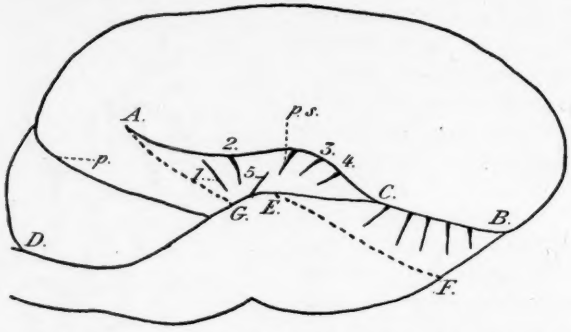


Fig. 17. Schéma destiné à montrer la constitution de la région télencéphalique operculisée chez le Zèbre de Grévy. 3/4 de G.N.

l'angle réel des rhinales *DEB* est beaucoup plus ouvert que son angle apparent *DEF*; dans les derniers stades de développement et chez l'adulte, c'est l'angle apparent que nous avons mesuré. Si nous avions mesuré l'angle réel, nous aurions constaté une augmentation d'ouverture progressive avec l'âge beaucoup plus grande encore que celle que nous avons signalée. Chez le Zèbre de Grévy qui nous a servi de type l'angle réel est par exemple de 153° au lieu de 138° pour l'angle apparent.

La région située dans l'angle *BEF* et garnie de plis radiaires dépend du rhinencéphale comme nous l'avons montré; c'est la lèvre inférieure de la rhinale. Au contraire, la région représentée par l'espace *GAC*, *AG* étant la limite antérieure de l'operculisation en avant, est néopalléale.

Dans cette région, nous voyons un petit sillon situé à peu près en face de l'angle des rhinales, mais qui ne l'atteint pas ou qui ne l'atteint qu'imparfaitement (nous avons vu son apparition au stade 9, Hémione), ce qui fait

que pour le voir on est obligé de réséquer la lèvre operculisante. Ce sillon dirigé de bas en haut et d'avant en arrière est la *pseudosylvia*; par conséquent, la région située en arrière de ce sillon jusqu'à la rhinale est le bras postérieur du *gyrus arcuatus* I de Leuret. La région située en avant est le bras antérieur de ce même *gyrus*, et, pour sa partie tout à fait antérieure qui n'est pas operculisée, la base du *gyrus reuniens*.

Les sillons 1, 2, 3, 4, sont des sillons de complication, les deux premiers du bras antérieur du *gyrus arcuatus* I, les deux seconds de son bras postérieur; 5 est peut-être une dépendance de la *pseudosylvia*, son segment inférieur séparé du segment supérieur et, en quelque sorte, décalé par rapport à lui.

Notons encore à-propos de la région operculisée que la branche postérieure de l'*ectosylvia* est ici en contact avec la rhinale postérieure contrairement à ce qu'on observe chez les Carnassiers (au moins chez ceux à territoire central complètement superficiel) où les deux sillons sont séparés par un large pli de passage.

La face interne de l'hémisphère ne présente à signaler que: 1°, l'indépendance du crucial par rapport à l'intercalaire en connexion au contraire avec le *genualis*; 2°, la présence d'un calloso-marginal bien développé.

Nous ne croyons pas utile de revenir ici sur les sillons qui existent entre l'*ectosylvia* et la *suprasylvia*, ni de nous arrêter à la description des plissements qui ne sont que de complication.

RÉSUMÉ

Nos observations embryologiques nous conduisent à considérer que le cerveau des Equidés est fondamentalement caractérisé

1°, par sa grande longueur par rapport à sa hauteur si on le compare à celui des Carnassiers. Ce caractère qui est commun à tous les Ongulés, abstraction faite de quelques exceptions très particulières, s'établit progressivement au cours du développement, le cerveau se rapprochant beaucoup plus au début que plus tard de la forme subsphérique;

2°, par la grande ouverture de l'angle de ses rhinales, ce caractère s'établissant aussi progressivement au cours du développement;

3°, par une operculisation qui porte en avant sur le *gyrus arcuatus* I de Leuret (*neopallium*) et en arrière sur la face supérieure du lobe piriforme (rhinencéphale), le sillon d'operculisation étant en avant l'*ectosylvia* et en arrière le segment postérieur de la rhinale postérieure. Chez les Carnassiers qui présentent une operculisation, celle-ci porte également sur le *gyrus arcuatus* I de Leuret, alors que chez les Primates elle intéresse en outre une partie du *gyrus arcuatus* II; mais chez les premiers comme chez les seconds il n'y a pas d'operculisation rhinencéphalique comparable à celle du cheval;

4°, par la présence d'un complexe sylvien (sillon γ) court et vertical (ce qui est en rapport avec le grand allongement et le grand surbaissement du

cerveau) dont les lèvres sont constituées au dépens du *gyrus arcuatus* II de Leuret;

5°, par la rectitude de l'*ectosylvia* et de la *suprasylvia*, caractère en rapport avec le grand allongement et le grand surbaissement du cerveau; chez les Carnassiers ces scissures sont fortement arquées;

6°, par le contact de la branche postérieure de l'*ectosylvia* avec la rhinale postérieure;

7°, par la très fréquente liaison au moins à la surface de la *presylvia* et de la *suprasylvia*, ces deux scissures n'étant séparées que par un pli de passage toujours étroit et le plus souvent situé dans la profondeur;

8°, par la brièveté du coronal le plus souvent relié à la surface à la *presylvia* et au crucial;

9°, par l'indépendance du crucial par rapport à l'intercalaire;

10°, par l'étroitesse du *gyrus* sigmoïde;

11°, par la liaison du *genualis* à l'intercalaire;

12°, par le grand développement du calloso-marginal.

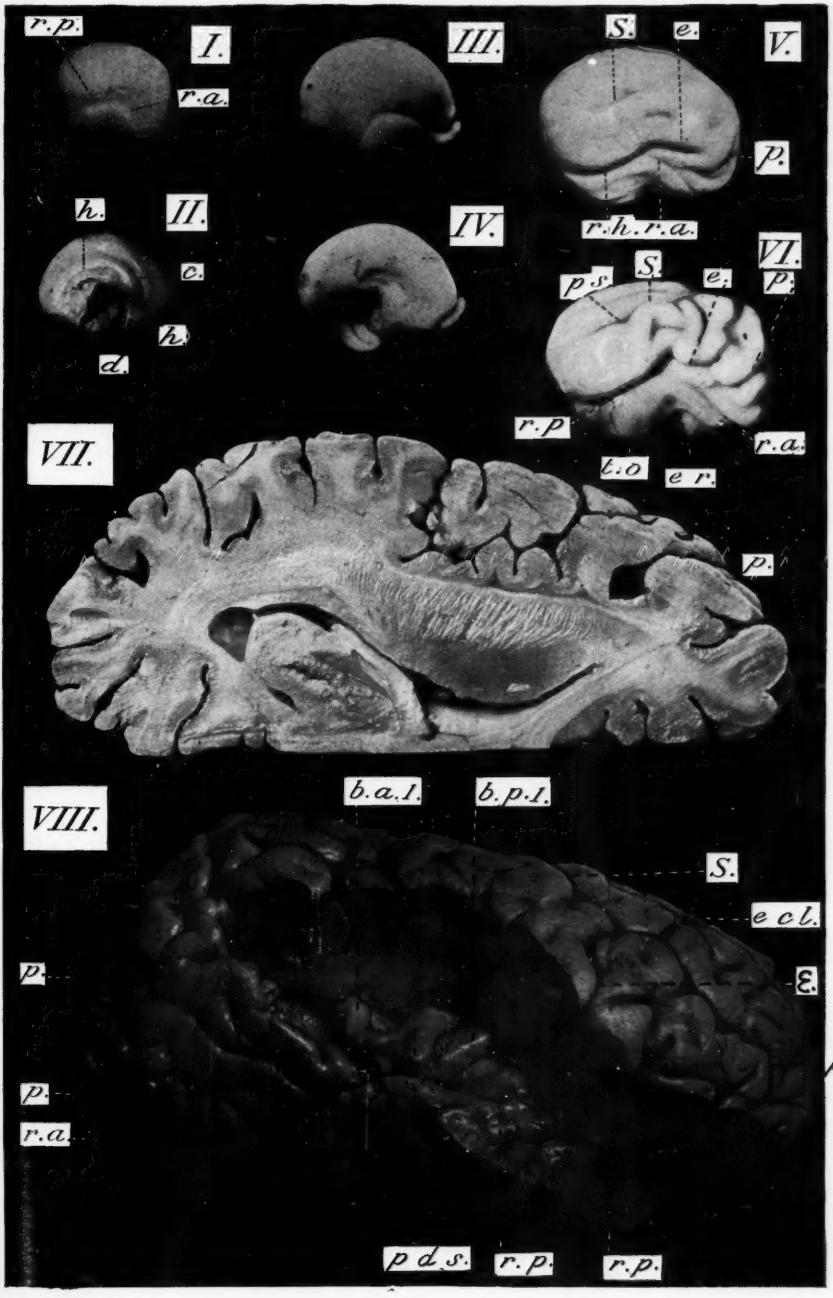
SIGNIFICATION DES LETTRES PORTÉES SUR LES FIGURES DU TEXTE ET DE LA PLANCHE

Rhinencéphale

R. rhinencéphale.
r.a. rhinale antérieure.
r.p. rhinale postérieure.
er. endorhinale.
t.o. tubercule olfactif.
s. *sulcus sagittalis.*
s.m. *sulcus sagittalis medialis.*
s.t. *sulci transversi gyri olfactorii lateralis.*
h. fissure hippocampienne.
d. *gyrus dentatus.*
f. *fimbria.*
f.p. *fissura prima* de His.
a. sillon innominé entre le *gyrus* et le *tractus olfactorii laterales.*

Neopallium

N. *Neopallium.*
S. *suprasylvia.*
ps. *postsylvia.*
e. *ectosylvia.*
p. *presylvia.*
l. latéral.
ecl. ectolatéral.
enl. entolatéral.
c. coronal.
x. crucial.
o. orbitaire.
c. calcarine
i. intercalaire.
g. *genualis.*
c.m. calloso-marginal.
ps. *pseudosylvia* (fig. 17).
β. dépression correspondant sur le *neopallium* au contact du cerveau moyen.
γ. encoche existant à la lèvre supérieure de l'*ectosylvia* au point où elle se coude (ébauche de complexe sylvien).
δ. encoche marquant l'extrémité légèrement relevée de l'*ectosylvia* (fig. 7, I).
ε. sillon oblique de Holl.
ζ. sillon vertical continuant la direction de l'*ectosylvia* mais en étant séparé par un pli de passage superficiel ou profond.
+ plis de passage.
p.p. pli de passage supra-présylvien, dans la figure 14 (III).
b.a.l. bras antérieur du *gyrus arcuatus* I de Leuret.
b.p.l. bras postérieur du *gyrus arcuatus* I de Leuret.


r.p.
I.
r.a.
III.
S.
e.
V.
p.
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II.
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h.
d.
IV.
r.h.r.a.
VI.
S.
p.s.
e.
p.
r.p
r.a.
VII.
t.o
e r.
p.
b.a.l.
b.p.l.
VIII.
S.
e cl.
p.
ε.
p s.
p.
r.a.
p d s.
r.p.
r.p.

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LÉGENDE DE LA PLANCHE

Fig. I. Stade No. 1. Individu sans numéro au même état de développement et ayant la même longueur de tête que le No. 1913-380. Face latérale externe droite du télencéphale. G.N.

Fig. II. Stade No. 3. No. 1929-15. Face latérale interne droite du télencéphale. G.N.

Fig. III. *Ursus* (*Thalassarctos*) *maritimus* Desm. nouveau-né ♀. Face latérale externe droite du télencéphale. G.N.

Fig. IV. *Ursus* (*Thalassarctos*) *maritimus* Desm. nouveau-né ♀. Face latérale interne gauche du télencéphale. G.N.

Fig. V. Stade No. 5. No. 1929-13. Face latérale externe droite du télencéphale. G.N. Sur cette figure lire *r.p.* au lieu de *r.h.*

Fig. VI. Stade No. 8. No. 1927-298. Face latérale externe droite du télencéphale. G.N. L'indication *t.o.* se rapporte à la région située au-dessous de *er*.

Fig. VII. Zèbre de Grévy. No. 1913-58. Section horizontale de l'hémisphère droit pratiquée parallèlement à la rhinale antérieure et à 1 centimètre au-dessus environ; pour montrer les rapports du *claustrum* et de la *presylvia* (*p.*). G.N.

Fig. VIII. Zèbre de Grévy No. 1913-58. Hémisphère droit, face externe. Section de la lèvre supérieure de l'*ectosylvia* et de la rhinale postérieure, pour montrer les régions néopalléale et rhinencéphalique operculisées. G.N. Sur cette figure au lieu de *p.* (immédiatement au-dessus de *r.a.*) lire *o.*

THE URACHUS: ITS ANATOMY, HISTOLOGY AND DEVELOPMENT

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A casual study of the current descriptions of the urachus, some of which form the basis of erroneous conceptions of pathology, will disclose a singular lack of harmony in essential points. It was considered advisable in order to elucidate the etiology of certain rare conditions encountered that a systematic study of the organ should be undertaken. This was carried out by means of an examination of twenty-eight consecutive specimens derived from the post-mortem room, from still-born foetuses and from preserved cadavers. Previous investigations of the same nature had been carried out by Luschka in 1862 (9) and by Wutz (19) in 1883. The findings of these anatomists have not been followed by the writers of English anatomy textbooks, so that the time seemed opportune for confirming or refuting them.

Without referring *in extenso* to the investigations quoted, it may be said that the authors denied that the epithelial lining of the urachus became obliterated in adult life to form a solid cord, but that the central canal with its epithelial lining persisted and sometimes communicated with the bladder. In addition, Luschka held that the urachus rarely reached the umbilicus in the adult, but on the contrary, "petered out in a series of fine thread-like cords before it reached that point." It is obviously of importance in order to understand urachal pathology to know whether one has to deal with a fibro-muscular cord or with an epithelially-lined canal and whether the structure developed from the foetal allantois or from the ventral cloaca.

UMBILICAL ARTERIES AND THE URACHUS AT BIRTH

These structures emerge from the umbilicus and it will be useful to recall the exact anatomy of the part. The anterior rectus sheath becomes continuous with the posterior sheath of its own side. The contact of the two rounded borders, so formed, fuse or are joined together by fibrous bands forming the linea alba which may be compared to the stitches uniting the seams of a coat. The umbilicus may be likened to a gape in the seam and leads to the space between the posterior sheath and the transversalis fascia. The latter is protruded like the finger of a glove through this gape or deficiency into the first centimetre of the umbilical cord. At this point, the glove finger is deficient at the tip, so that the protrusion of fascia forms a tunnel by which

the umbilical vessels and the fibrous remains of the allantois are conducted through skin, subcutaneous fascia and linea alba into the space between the transversalis fascia and the peritoneum. Viewed from within, the urachus at birth is a tiny structure hugging the anterior abdominal wall and is overlapped and almost concealed by the relatively enormous umbilical arteries. The latter project markedly inward, their diameter being 5 to 7 mm. At this stage the length of the urachus is 2 to 2·5 cm. from the apex of the bladder to the umbilicus, to which must be added half a centimetre for its intramural course in the bladder wall. The diameter at the bladder end averages 3 mm. but in the greater part of its course only 1 mm. The two umbilical arteries and the urachus, forming a kind of tripod, are met by the large umbilical vein 1 cm. in diameter, all passing through the tunnel of transversalis fascia already mentioned.

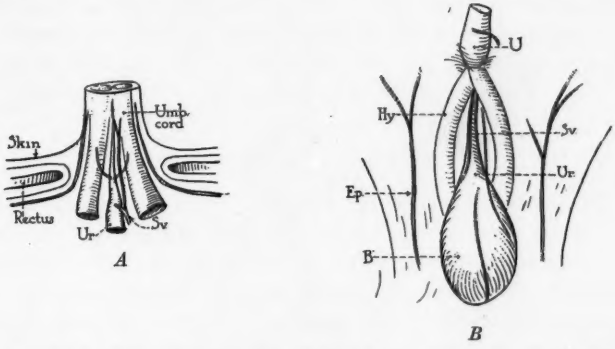

Fig. 1. The structures about the umbilicus in a full-time foetus viewed from the peritoneal aspect. *B* gives a general view of the bladder and urachus, and *A* illustrates the upper termination of the urachus. *B*, bladder; *Ep*, a branch of the epigastric artery; *Ur*, urachus; *Sv*, urachal artery; *Hy*, umbilical artery; *U*, umbilical vein.

Of considerable importance in connection with the descent of the urachus to be described later, is the method of its termination at the upper end. Here it divides into a number of fibrous strands usually three (fig. 1 *A*). One of these is attached to, and continuous with, the adventitia of each umbilical artery; the third or middle strand passes through into the umbilical cord and breaking up into numerous fine strands is lost at a point 1 cm. from the body surface. These strands represent the only remains of the obliterated allantois. The attachments to the umbilical arteries are almost invariably distinguishable in the adult and serve as landmarks to indicate the upper limits of the urachus proper.

DESCENT OF THE URACHUS

The common conception of the change that takes place in the urachus after birth, is that the canal is obliterated from above downwards, but that in the adult it still maintains its attachment to the umbilicus. This theory cannot be made to fit in with the embryological or anatomical facts. On the contrary, the urachus, developing as the upper part of the bladder, descends with this organ so that its apex leaves the umbilicus and later is found far down towards the symphysis pubis. The process that occurs is apparently the following: at birth the apex of the bladder is 4 cm. above the symphysis, and as it rapidly descends it pulls the urachus with it. The latter being attached to the umbilical arteries drags the obliterated ends of these with it so

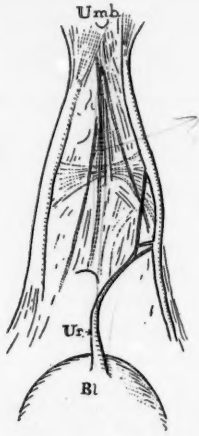

Fig. 2. The peritoneal aspect of the urachus in an adult male, age 56. Note the fibrous strands of "Luschka's plexus." The urachus has been pulled over during its descent and is attached to the left umbilical artery only. *Bl*, bladder; *Ur*, urachus; *Umb*, umbilicus.

that an anchor-like arrangement is formed about 3 cm. above the bladder apex. In one specimen examined there had apparently been no such attachment, and the round occluded ends of the arteries lay free, one on either side of the upper end of the urachus. The adventitia of the arteries and the apex of the urachus usually become involved in the extensive fibrous tissue which marks the closure of the umbilical fascial tunnel, and the production of the umbilical scar. As the arteries and the urachus are dragged down by the bladder descent, this tissue is drawn out into a fibrous cord. More commonly the adventitia of the arteries is teased into a multitude of fibrous strands which may be seen in most adult subjects radiating from the umbilicus. This was observed by Luschka who described it as a "fascial plexus." A common variation is where the attachment to one artery has been stronger than that to the other so that the urachus is pulled markedly to one side (fig. 2). This

"plexus" which is much commoner than a single fibrous cord, becomes much more marked in cases where abdominal distension due to pregnancy or ascites has occurred, and reaches a lateral spread of as much as 3 inches. The individual threads frequently reassemble just below the umbilicus forming a central cord which has been mistaken for the urachus, the latter really terminating as much as 10 cm. lower down.

In this teasing out process, the urachus itself being attached on either side is torn asunder and doubtless the epithelial cells which always exist in its centre are separated and give rise to the cystic adenomatous masses which sometimes occur in this situation, in a similar manner to the formation of "inclusion" cysts by the burial of dermal epithelium (Plate I, figs. 1, 2). Further than this, the splitting in the 33 per cent. of cases where the urachal canal communicates with the bladder may liberate tiny drops of urine into the transversalis-peritoneal space and give rise to septic effusions. These are strictly localised between the fibrous strands of Luschka's plexus which gain attachment to both peritoneum and fascia shutting off the space into a large number of compartments.

ANATOMY OF THE ADULT URACHUS

The true upper extremity of the urachus was determined not only by noting the point of junction with the obliterated umbilical arteries or some portion of them, but also by cutting sections at various levels. For some distance above the bladder the urachal canal, as observed in sections, is so characteristic as to be unmistakable (Plate I, fig. 3). Even at higher levels, and, at birth right up to the umbilicus, the canal, even if partially obliterated, has a characteristic whorled arrangement, while once the first attachment to the artery is passed, the sections show merely normal fibrous tissue, clearly proving that at this point the urachus ends. The fibrous strands that carry out the partial obliteration which is always confined to a small segment at the upper end are longitudinal in direction and appear in cross-sections as bundles cut transversely. Each of these bundles corresponds to one of the tiny cell columns into which the main block of central epithelium breaks up as a prelude to obliteration (Plate II, fig. 2). The adult urachus extends upwards from the anterior border of the bladder, usually arising 5 to 10 mm. below the apex, very occasionally from the apex itself, and still more rarely from the superior surface close to the apex. Its extreme limits in length are 3–10 cm. but in the vast majority of cases it is 5–5·5 cm. (The average distance from umbilicus to bladder apex is 16–18 cm.) Where it leaves the bladder it is broad and somewhat flattened from before backwards. Here its breadth is 8 mm. and it tapers to 2 mm. at the apex. It lies between the transversalis fascia and the peritoneum in the space of Retzius and is surrounded by loose areolar tissue, being freely mobile in its lowest part to allow it to move with the expansion of the bladder. At its apex it is more firmly attached and closely

applied to both peritoneum and fascia. In no case was a mesentery present though Binnie(1) maintained that one always existed at an early stage of development.

BLOOD SUPPLY

The blood supply of the urachus is definite and has a bearing on certain pathological features of congenital umbilical fistula. It can best be observed in the foetus (fig. 1). One of the superior vesical arteries, usually the left, passes up the lateral aspect of the bladder to the apex. After giving off its branches to the bladder it courses along the ventral aspect of the urachus, being closely applied to it and supplying it with branches. This vessel is so constant that it may be described as the urachal artery (fig. 1, *Sv*). It can be traced right up to the apex of the urachus and along the allantoic remains as far as the junction of the umbilical cord with the skin and in some instances even into the cord itself. In cases of congenital urinary umbilical fistula this artery causes increased vascularisation of the first part of the cord which prevents the onset of dry gangrene in virtue of which the cut cord normally separates—the separation does not take place—and the large red tumour which forms such a remarkable feature of these cases is left projecting from the navel. The urachal artery anastomoses in the region of the umbilicus with the terminal branches of the superior vesical artery of the other side and also with branches of the epigastric arteries which re-pierce the transversalis fascia from without inwards.

HISTOLOGY OF THE URACHUS

This account is based on a study of specimens by means of serial sections and the dissecting microscope. They have also been compared with the observations of Luschka(9) and Wutz(19). On one point all observations harmonise, viz. that the epithelial canal persists throughout life and is never completely obliterated. The lumen is, however, subject to interruption by filling with desquamated cells from the inner layer. These cells unlike those which are always being desquamated into hollow viscera such as the bladder have no outlet and so accumulate in the canal at intervals, and by their degeneration form a cast which, in parts, completely fills the lumen (Plate II, fig. 1). The canal is, as a rule, sacculated at various points (Plate II, fig. 3), and tiny cysts due to cell proliferation and degeneration formed. The epithelial cells, however, far from being destroyed display a remarkable activity in reproduction and multiplication, pushing out into the connective tissue when they can no longer find room in the canal. As the result of this process small adenoma-like structures and cysts are the rule rather than the exception, and this phenomenon is more marked after the age of fifty. This point requires emphasis, as in such an authoritative textbook as *Cunningham's Anatomy* (p. 1314, 1922 ed.) the

following statement occurs: "This part of the cloaca (the urachus) loses its lumen about the fifth week," and again: "The epithelium of the urachus completely disappears." In reality, it is doubtful if there is in the body any better example of the remarkable persistence of epithelium in rudimentary structures, or of its renewed activity in adult life. The urachus grows very little after birth, the average length being in the adult and the child 5 cm. and 2·5 cm. respectively. It appears also to undergo but slight obliteration of its canal after birth—as it is in the new-born child so it will remain in the adult. In only one specimen examined was actual capillary invasion with

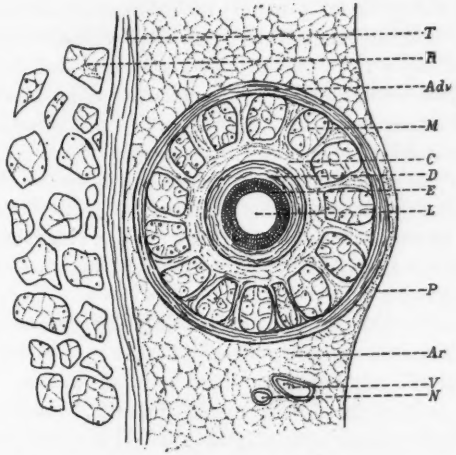

Fig. 3. A diagrammatic cross-section of the urachus *in situ*. *T*, transversalis fascia; *R*, rectus abdominis; *Adv*, connective tissue layer or adventitia; *M*, muscle layer showing longitudinal bundles in section with fibrous tissue between them; *C*, loose connective tissue surrounding the urachal canal; *D*, dense fibrous tissue forming outer layer of the urachal canal; *E*, epithelium; *L*, lumen of urachal canal; *P*, peritoneum; *Ar*, loose areolar tissue surrounding urachus; *V*, urachal vein; *N*, urachal artery.

the formation of fibroblasts seen in progress and that close to the upper extremity. The urachus (fig. 3) has a serous coat (peritoneum) on its dorsal surface only, and this is deficient where it pursues an intramural course of 1 cm. in the wall of the bladder. Next to the serous lining from without inwards is a loose areolar and then a fine connective tissue layer. The comparatively thick adventitial coat of the bladder is not prolonged to cover the urachus. It is a somewhat striking circumstance that the outer coat of the bladder forms a collar-like deficiency through which the urachus ascends. Here there is a relatively weak point in the bladder wall, and several examples of diverticula have been observed. The next layer of the urachus is formed of muscle fibres which arise in a very definite fashion from the bladder. Two bands of longitudinal muscle fibres sweep like broad straps from the prostate

in front to the prostate behind (Schafer, *Quain's Anatomy*, vol. XI, pt 1). They pass on either side past the urachus contributing no fibres to it. When the bladder is being emptied the contraction of these bands brings their medial margins firmly together forming a strong support in the moment of danger for the weak point of the urachal insertion, just as the contraction of the recti support the weak middle line of the abdominal wall. Superficial to the longitudinal bands are other fasciculi which run more or less obliquely. Many of their fibres pass up the urachus, giving it a complete investment in the lower part, but gradually thinning out as they ascend. By their attachment to the upper fibrous part of the structure they form a kind of musculo-tendinous apparatus. From this point of view the urachus may be considered as a muscle whose tendon gains attachment to the umbilical region through the medium of fibrous cords derived from the umbilical arteries. That its purpose is not that of a mere passive suspender of the bladder apex is suggested by the tortuosity of the canal in its intramural part (fig. 4), indicating that the structure undergoes lengthening and shortening in life. It is probably analogous to the musculi papillares of the heart. It takes in the slack as the bladder empties just as in emptying a rubber hot water bottle one lifts up the bottom end to prevent it flapping over and so hindering the outflow, or as the Arab attaches a string to the closed end of his water skin to facilitate the outflow of its contents.

Another function of the urachus is suggested by the manner in which its muscular fasciculi spread out in cone-shaped fashion over the bladder gaining an attachment to the prostate all round. Thus the urachus may give a *point d'appui* for the contraction of these muscle bundles, whereby the bladder is compressed uniformly from without and steadied while the strap-like bands of the detrusor urinae are acting.

Deep to the muscle wall of the urachus and intimately connected with it is a dense stratum of fibrous tissue, and internal to that again a layer of somewhat loosely arranged connective tissue. So loose is the latter, that the central urachal canal can easily be dissected out and appears as a white tubular structure of uniform bore. The pyramidal appearance of the urachus as a whole is in no way reflected in this tube which resembles a small thoracic duct. Its usual diameter is 1 mm. It can be traced almost from the upper end of the urachus, and as stated before pursues a tortuous course through the muscular wall of the bladder, till it reaches the external surface of the mucous membrane To this point it can always be traced with the greatest facility, but its manner of ending is subject to considerable variation (fig. 4). In a certain number of cases it communicates directly with the bladder, its epithelium becoming continuous with that of the latter organ. In others it ends in a number of fibrous strands which lose themselves in the submucosa, while again it may terminate in a cystic dilatation. The urachal artery does not follow the canal in its intramural courses but joins the urachus external to the bladder wall.

THE MINUTE STRUCTURE OF THE URACHAL CANAL

The urachal canal proper (fig. 3) is but loosely connected with the muscular and fibrous portion of the structure by areolar tissue, and consists of two layers—an outer coat of condensed fibrous tissue (fig. 3, *D*) and an inner one of epithelium (fig. 3, *E*). The outer coat displays evidence of proliferation where it abuts on the lining of epithelium, one or two rows of young fibroblasts forming a whorled arrangement around the latter (Plate II, fig. 1). These are in direct contact with the outermost layer of epithelial cells, no basement membrane intervening. The epithelium, is as a rule six or seven layers deep, though there may be no more than two. It has rarely the regular structure of transitional epithelium, the deep cells being of the same type as the superficial. Occasionally pear-shaped cells may be seen or a single cell with more than one nucleus is present. Sometimes the nuclei of the outermost layer of cells lie with their long axes at right angles to the diameter of the canal, but more commonly are in the same line. The cells next to the lumen show a tendency to desquamate and become free, and sometimes they accumulate and almost plug the lumen. It is noteworthy that in those cases in which there is a communication with the cavity of the bladder, the lower part of the lumen remains free, as the desquamated cells pass into the bladder and escape with the urine.

The nuclei are vesicular, oval, and stain lightly. They average 12 μ in length and 9 μ in breadth. There is a definite nucleolus, sometimes two, and a loosely arranged chromatin network. Division by an amitotic process is frequently observable but there is an absence of clearly defined mitotic figures. The thickness of the epithelial lining is rarely uniform, the cells being heaped up at one segment to ten or twelve layers, while at others there are only two or three (Plate II, fig. 1). The size of the lumen varies from a mere slit to a canal fully half a millimetre in diameter and appears to bear no constant ratio to the age of the subject. The general thickness of the epithelial part increases slightly with age, and the canal is longer in the adult than the child, proving that a certain amount of proliferation is taking place. As Luschka previously observed (*loc. cit.*) the epithelial tube does not remain central in relation to its fibrous covering throughout the whole course, but deviates from side to side as it ascends.

It gives rise also to numerous small pockets or diverticula. These latter, however, owe their rise not to simple dilatation but to the degeneration of masses of epithelial cells which have become detached from the central epithelium. These give rise to small adenomatous formations or by central degeneration to tiny cysts. The canal is between 3 and 7 cm. in length or practically coterminous with the urachus as a whole. At the lower part it is sufficiently pervious to receive a fine bristle but higher up its potency is interrupted by accumulation of desquamated cells, by the epithelium of one side meeting that of the other, or by the central core of epithelium splitting up into several smaller cores (Plate II, fig. 2). It may be patent above and

below and impervious in the middle, or be shut off into numerous pervious sections like a bamboo cane.

CONTENTS OF THE URACHAL CANAL

Luschka described the contents of the canal as consisting of pigmentary, fatty, and amyloid substances, the products of cell degeneration, also of fat molecules and corpora amylacea. The latter bodies are of great interest as tumours of the urachus resemble prostatic tissue, and Nicholson (11) has observed amyloid bodies in them. There seems little evidence that the epithelial cells of the urachal canal can give rise to a true secretion. I have seen numerous cells of the goblet type in a malignant tumour of the urachus but never in a simple tumour or a normal organ. I believe that cysts due to such a cause never arise. The only true type of urachal cyst is that formed by the proliferation of epithelial cell masses and their breaking down in the central parts. A certain amount of obliteration of the urachal canal from above downwards appears to take place occasionally throughout life as witnessed by the discovery even in subjects of over fifty years of vascular granulation tissue invading and replacing epithelium. This process however is rare, never reaches very far down and is accompanied in many instances by increased epithelial growth. The detachment of cells during this process leads to those curious adenomatous formations referred to above, and found so commonly in the adult urachus (Plate I, fig. 2).

METHOD OF TERMINATION OF THE LOWER END OF THE URACHUS AND ITS RELATION TO THE BLADDER

The constant presence of a pervious urachal canal at all ages having been established, it is of great interest to ascertain in what percentage of cases there is a direct communication between it and the bladder and how in these cases the urine is prevented from passing up through the orifice.

The question is not new. Peyer at the end of the seventeenth century maintained in opposition to Caspar and others that there was a communication between the urachal canal and the bladder during the foetal period. J. G. Walker (17) stated in 1775 that this communication was present at all stages of life and would admit a fine probe. Wutz (19) considered that the opening existed in most cases and described a small transverse fold of mucous membrane which prevented regurgitation of urine. Later writers, notably Doran (3), have discussed the presence of this "valve of Wutz" in relation to vesico-umbilical fistula. The subject was approached in the present investigation by making a minute examination of the uracho-vesical junction and by attempting to pass fine bristles or inject methylene blue under pressure, with subsequent examination of longitudinal and serial transverse sections. In seven out of twenty-one specimens examined in this way there was a connection between

the urachal canal and the bladder through which a fine bristle could be passed (i.e. 33⅓ per cent.). In the remaining fourteen (or 66⅔ per cent.) microscopic sections showed that there was an absence of this communication. In only one of the first series was there a "Wutz valve" guarding the orifice (see fig. 4).

A careful examination was also made in most of the surgical museums of Edinburgh and London of all bladder specimens. A large proportion of these cases had suffered from obstruction to outflow of urine, and about the same percentage (33⅓ per cent.) showed the vesico-urachal orifice, frequently much dilated.

A third method of approach has been by examination in some hundreds of cystoscopic examinations, but in these, possibly from the difficulty in placing the cystoscope so as to get a close-up view and the necessary magnification, not nearly the same proportion of orifices was observed. The urachovesical orifice could be divided into four main types. In the commonest (three dissection cases) there was no depression or papilla, the opening being flush with the mucous surface (fig. 4 *B*). The second method (two cases) was where the mucous membrane of the bladder was protruded in the form of a diverticulum, between the fasciculi of the bladder muscle, presenting much the same puckering of mucous membrane at the bladder orifice as is seen in a pathological diverticulum. Into the sacculus the canal of the urachus opens. I have seen this form several times in otherwise normal bladders with the cystoscope and a beautiful specimen of it exists in the Royal College of Surgeons, Edinburgh (Spec. 28, 50).

A case where such a diverticulum was pathologically enlarged and contained a calculus was reported by Campbell Dykes (4).

In the Royal College of Surgeons Museum, London, specimens 3728, 3721 *a*, 2232 and 2223 all show a protruding pouch of this nature.

The third method (one case, fig. 4 *A*) was where the orifice opened at the apex of a pyramidal projection. A beautiful illustration of this is shown in specimen 3730 in the museum of the Royal College of Surgeons, London, described in the catalogue as "a papillary projection of unknown origin."

The fourth method (one case) was where the opening was at the bottom of a dimple 3 mm. in depth and diameter. In all these cases the continuity of urachal and bladder epithelium was shown by sections. In none of them would a bristle or a blue injection pass in more than 1 cm. owing to the blocking of the otherwise patent canal with epithelial debris at this point, though microsopic examination showed continuity of epithelium and patency at the higher level. It is noteworthy that this is about the extreme depth of the dilated canal in cases of urinary obstruction, an observation which shows the improbability of the re-opening of the whole length of the canal in adult life.

Such an acquired umbilical fistula is an impossibility on anatomical grounds.

In several cases where no actual communication existed a slight depression (fig. 4 *D*) or red spot on the bladder mucosa marked the point opposite the urachal insertion. In all cases the fibro-epithelial canal could be traced as far as the outer surface of the bladder mucosa.

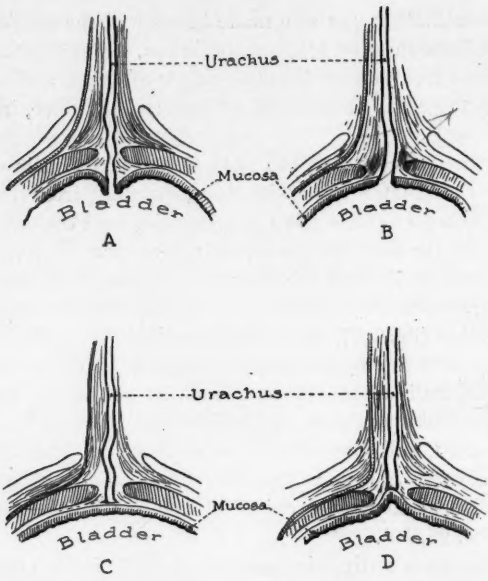

Fig. 4. Different methods of termination of the lower end of the urachus. In *A* it communicates directly with the bladder ending on the summit of a papilla; in *B* the terminal opening is flush with the bladder mucosa; in *C* and *D* it reaches the outer surface of the bladder mucosa but does not communicate with the lumen. In *D* a dimple in the vesical mucosa indicates the point of attachment of the urachus. Note the tortuous course of the urachal canal.

DEVELOPMENT OF THE URACHUS

It appears now to be universally conceded that the allantois takes no share in the development of the bladder which is partially cloacal and partially Wolffian in origin. Similar agreement has not hitherto been reached in regard to the urachus. Sir Arthur Keith (8) maintains its origin from the allantois. W. Felix (7), however, writing in Keibel and Mall's *Human Embryology* maintains that the apex of the ventral cloaca is carried in a cephalic direction with the umbilicus and that its upper part is obliterated to form the urachus. He says: "In man a ventro-cloacogenic and mesodermic bladder develops, an allantoidiogenic origin such as was formerly supposed to occur does not exist. A view of the anterior abdominal wall from behind (in embryos of 10–24 mm.) shows that the two umbilical arteries bound a triangular area—the vesical

plate whose apex is of course formed by the umbilicus (see fig. 1 *A*). Within this area the bladder lies in such a way that its cranial apex reaches the umbilicus where it is connected with the remains of the allantoic stalk. This position the bladder retains at birth except that its apex diminishes more and more and finally becomes the urachus, this structure being accordingly a product of the bladder, i.e. of the cloaca and not of the allantoic stalk." Prof. Arthur Robinson (20) supports this view.

No doubt in some animals, such as the horse, the apex of the bladder reaches to the umbilicus and so-called urachal (really vesical fistula) is not uncommon in foals. There seems little doubt that this is the correct view, and the question is of considerable importance in refuting the common explanation of umbilical urinary fistulae, which are mostly in reality due to the lack of formation of the urachus and not to its patency. The essential similarity of the epithelia of the urachus and bladder and the arrangement of the muscle and fibrous coats of the two organs strongly support a common origin.

Further evidence is available also from the pathological side which need not be elaborated here. G. W. Nicholson (11) as the result of an exhaustive research laid down the rule that all the normal glands of the cloaca as well as those formed in pathological conditions are of one type and similar to prostatic glands. The type of so-called adenomatous tumour that develops in the bladder wall is amply illustrated in miniature in the urachus in a large proportion of adult subjects over fifty years of age as well as in several more gross tumours, simple and malignant, that have been observed. Thus on all grounds the conclusion is inevitable that the urachus is the modified—not obliterated—upper end of the foetal bladder. Only on this supposition can a rational explanation be given of umbilical urinary fistula. The only remains of the allantois in the full-time foetus is the central of the three fibrous bands attached to the upper end of the urachus. This band has been referred to early in the present article. It passes out between the umbilical arteries to be lost in the tissue of the umbilical cord (fig. 1 *A*).

ANOMALIES OF THE URACHUS

The most important anomalies are: (*a*) of formation; (*b*) of descent.

(*a*) In the anomalies of formation, the upper part of the ventral cloaca does not narrow, so that a true functional bladder reaches the umbilicus at birth. A gross example of this occurs in cases of extroversion of the bladder. In rare cases with the separation of the umbilical cord, this bladder discharges urine at the umbilicus. In others, the bladder descends so that in the adult its apex is conical and reaches as far as the normal apex of the urachus. This condition is familiar to gynaecological surgeons, and endangers the bladder in low laparotomy. Imperfect formation without descent may give rise to permanent umbilical urinary fistula, or the urine may break through

at the umbilicus in adult life owing to obstruction to urethral outflow. This is one of the forms erroneously called "acquired urachal fistula[1]."

(*b*) The urachus is normally formed but the urachus and bladder do not undergo descent. In this case also the apex of the bladder is close to the umbilicus and connected to it by the urachus. I believe this form is excessively rare, and is not a cause of umbilical fistula as the normal urachal canal is so narrow and so blocked with debris that no pressure of urine would ever penetrate its length.

The relation of these anomalies to pathological conditions is dealt with elsewhere and is not a suitable subject for an anatomical paper.

SUMMARY

The urachus is developmentally the upper part of the bladder, both being derived from the ventral cloaca. This part of the bladder narrows more and more, but retains in miniature its essential structure and at birth is still attached to the umbilicus. It is then known as the urachus, and in about two individuals out of three its lumen is separated from that of the bladder proper by a thin partition of mucous membrane which has grown in. In the remainder no such partition has developed. The urachus shares in the post-partum descent of the bladder, and in the adult is a cone-shaped structure 5·5 cm. in length passing up from the bladder apex, and attached to the umbilicus only by adventitial bands derived from the umbilical arteries which it has pulled down in its descent. Like the bladder it has a peritoneal and an extra-peritoneal surface and has the transversalis fascia on its outer and the peritoneum on its inner surface. The lumen of the urachus remains patent throughout life, though it may be plugged in places by masses of epithelial cells which have desquamated from the walls of its canal.

Being a vestigial structure, though of use as a musculo-tendinous adjunct to the bladder, it does not grow in proportion to the development of the body or bladder. It is only twice the length in the adult that it is in the newly born. There is little or no tendency towards the obliteration of its canal by fibrous tissue. The epithelium of the canal is an irregular form of transitional epithelium and displays great activity in cell division. On this account, groups of cells are pushed out into the connective tissue lining the canal, and by their degeneration form detached cysts or cystic diverticula of the lumen. After the age of fifty the continuance of the process causes the formation of quasi-pathological, and in rare cases grossly pathological, phenomena in the form of cystic adenomata of the prostatic type. Anomalies in the development of the urachus are responsible for occasional cases of urinary fistula at the umbilicus. These are all congenital in nature though symptoms may not develop till late in life.

[1] A case was observed in a child of two in which it appeared that the urachus had not formed and yet the bladder had descended to the normal level. The most exhaustive search within and without the bladder failed to discover any traces of a urachus.

Fig. 1

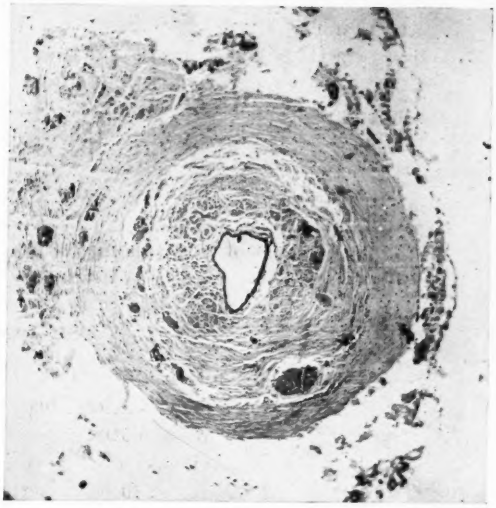

Fig. 3

Fig. 2

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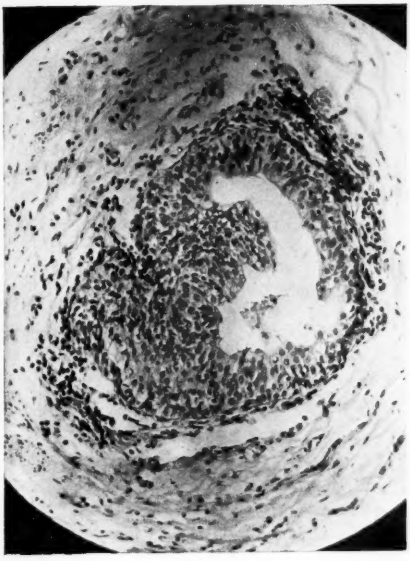

Fig. 1

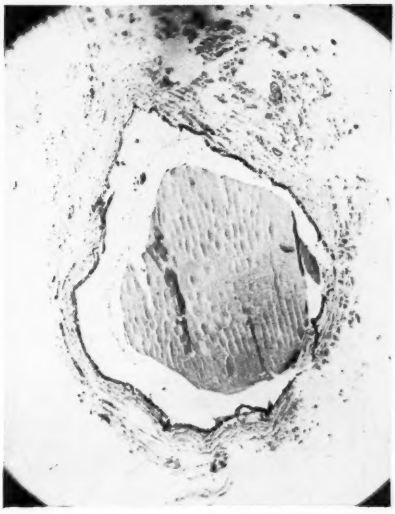

Fig. 3

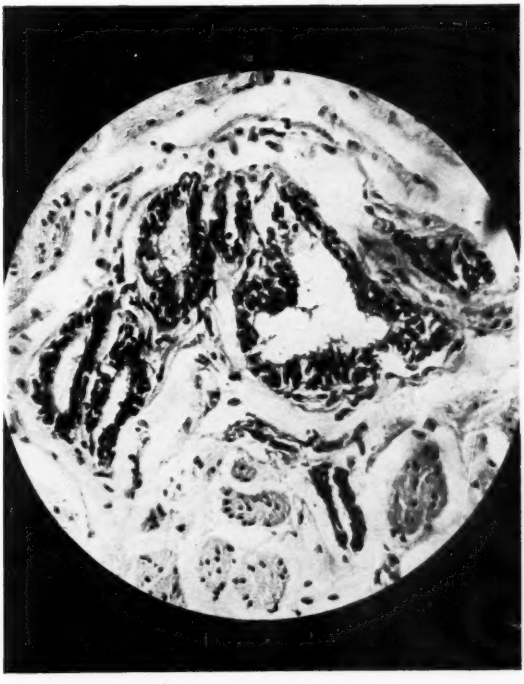

Fig. 2

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DESCRIPTION OF PLATES I AND II

Plate I

Fig. 1. A low power view of cystic formation found in the midline two centimetres below the umbilicus in a child of four years dying of tuberculosis meningitis. The urachus had descended and formed with the two obliterated umbilical arteries an anchor-like arrangement 3 cm. above the bladder apex. Possibly the structure illustrated which is of the adenomatous type was derived from epithelial cells shed from the urachus during its descent. Similar types of structure may be found lateral to the urachus near the bladder.

Fig. 2. A high power view of the upper part of the cystic structure.

Fig. 3. A low power view of a cross-section of the urachus of a male of 62 years, 2 cm. above the bladder apex. The thin epithelium of the canal with its distinct lumen can be clearly seen. (× 60.)

Plate II

Fig. 1. A high power view of the urachus showing the many layers and irregular distribution of the epithelial cells, some of which are lying free in the lumen.

Fig. 2. A cross-section of the upper end of the urachus in a male aged 56. The section is a transverse one 5 cm. above the bladder apex. The urachal canal which had a single lumen in its lower part has now broken up into seven separate canals. Serial sections above the level shown showed that the lumen became still further divided and was finally represented by small solid columns of cells, which gradually became replaced by young fibroblasts.

Active capillary invasion and fibroblast formation was taking place leading to obliteration of the extreme upper end of the urachus, 7 cm. from the bladder.

Fig. 3. Section through a cystic dilatation 2 cm. above the bladder in a male subject 60 years of age. The cyst is lined by two layers of epithelial cells and the lumen is filled with homogeneous material which has shrunk away from the walls during the preparation of the specimen. The presence of faintly staining nuclei suggests that the content is formed from broken down cell detritus. (× 60.)

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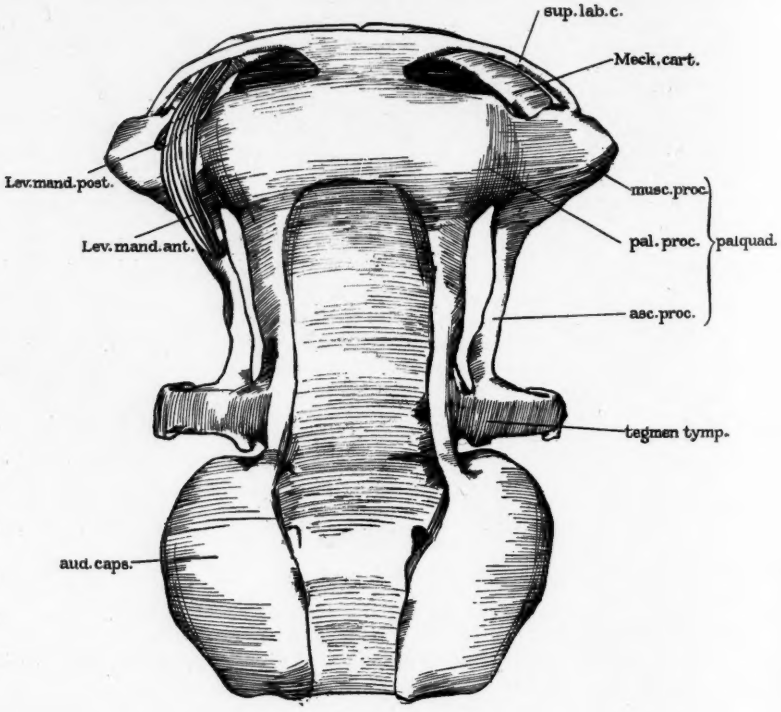
ON THE MASTICATORY AND HYOID MUSCLES OF LARVAE OF *XENOPUS LAEVIS*

By F. H. EDGEWORTH, M.D.

The masticatory muscles of the adult stage of *Xenopus* were described by Luther in 1914, but—as far as I know—no account of those of the larval stage has been given.

W. K. Parker, however, in 1876, published a description, illustrated by many figures, of the chondrocranium of *Xenopus* s. *Dactylethra capensis*. On



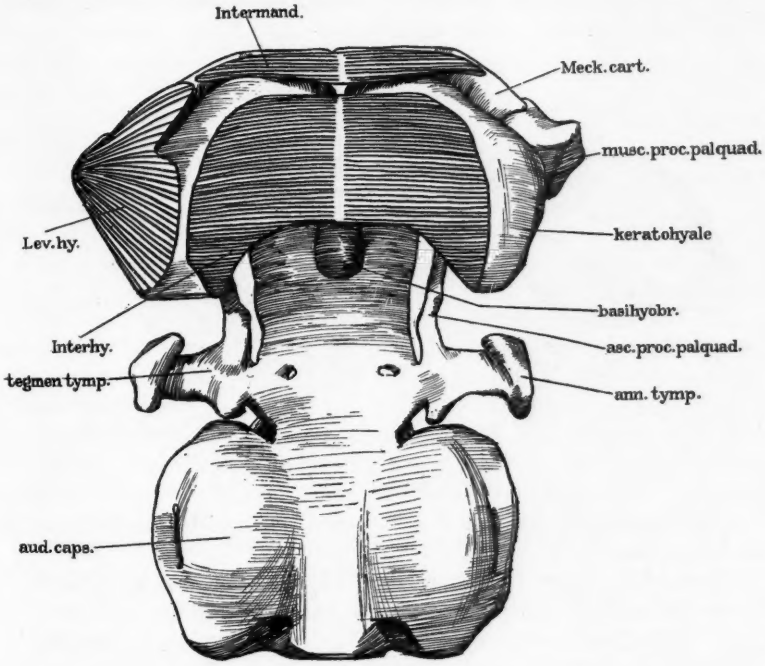
Dorsal aspect.

reading this, a few years ago, and learning that the mouth is terminal and wide, that there are no horny teeth, and that Meckel's cartilages are long and almost transverse in position, I thought that the mandibular and hyoid musculature might be less modified than in larvae of *Anura phaneroglossa*.

Professor J. T. Wilson kindly gave me two larvae, 17 mm. long, of *Xenopus laevis*, to test this theory. They were a part of the "Bles bequest" to the University of Cambridge.

The chondrocranium of these specimens is similar to, but not identical with, that of *X. capensis* described by Parker.

The palatoquadrate is horizontal in position and fixed to the chondrocranium by a short, broad, transversely directed, palatal process, and by a slender ascending process. The dorsal end of the latter is continuous with the dorsal end of the tegmen tympani. The processus muscularis is short and



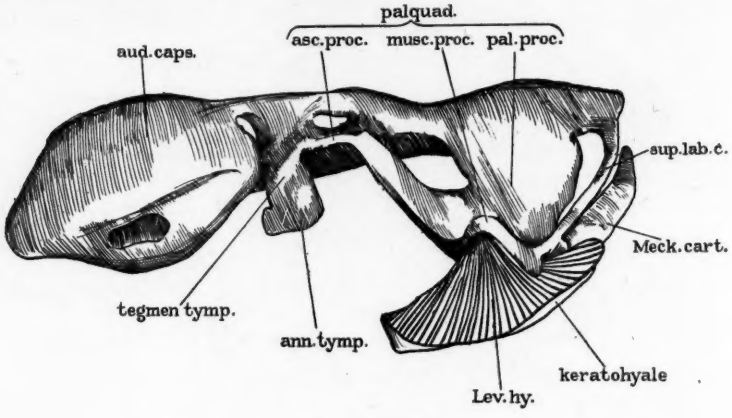
Ventral aspect.

blunt. The superior labial cartilage is a very slender bar which passes from the anterior end of the chondrocranium to the processus muscularis. In *X. capensis*, where—unlike *X. laevis*—there is a long labial tentacle, the superior labial cartilage does not join the processus muscularis, but is continued back to the extremity of the tentacle.

Meckel's cartilage is long and almost transverse in position. The outer end articulates with the anterior end of the palatoquadrate. The inner end meets that of its fellow. There are no inferior labial cartilages such as occur in *X. capensis*.

The hyobranchial skeleton consists of a long basihyobranchiale, with a hyoid and four branchial bars, on either side. The hyoid bar consists of a broad, thin, keratohyale. Its outer end articulates with the palatoquadrate just behind Meckel's cartilage. Its inner end meets the anterior part of the basihyobranchiale. The four branchial bars form a broad, thin plate, which is perforated by the 3rd, 4th and 5th gill-clefts[1].

There are two horizontally situated masticatory muscles—the Levatores mandibulae anterior and posterior. Both arise from the dorsal surface of the palatoquadrate and pass forwards to the external end of Meckel's cartilage. The Levator m. anterior is much the larger, arises further back, and in a dorsal view, covers the Levator m. posterior.



Lateral aspect.

The Intermandibularis is a simple narrow band which joins its fellow in a median raphé.

The hyoid muscles consist of a Levator hyoidei and an Interhyoideus. The former takes origin from the processus muscularis of the palatoquadrate, passes down fan-shaped, and is inserted into the keratohyale and Meckel's cartilage. The Interhyoideus is a broad, thin sheet. It arises from the keratohyale, passes inwards, and joins its fellow in a median raphé. The Interhyoidei, in a ventral view, cover the anterior part of the basihyobranchiale and the ventral portions of the keratohyalia.

The mandibular and hyoid muscles in larvae of *Anura phaneroglossa* are now well known. They were described by Dugès (1834), Schultze (1892), and by Luther (1914). I gave a description of their development in 1925.

Luther stated that the peculiar cranial features of larvae of *Anura phaneroglossa* are the result of considerable secondary modifications, and have no "ancestral value." He suggested that the cause of these modifications is to be found in the great length of the intestine—an adaptation to vegetable food—

[1] The branchial bars are not shown in the model.

which brought about a ballooning of the peritoneal cavity and its forward extension. This produced a forward migration of all organs lying in front of the peritoneal cavity and below the chondrocranium. The influence of the elongation of the intestine is probably not direct and mechanical, but hereditarily fixed.

The mandibular and hyoid skeleton of larvae of *Anura phaneroglossa* resembles that of *Xenopus*, and the masticatory muscles are similarly horizontal in position. But, there are differences. In larvae of *Anura phaneroglossa* the Levatores mandibulae anterior and posterior of early stages soon develop into the muscles which persist in adult life, and not—as in *Xenopus*—only at metamorphosis. Further, the Levator mandibulae posterior sublimis, the Levator mandibulae subexternus and the Levator mandibulae lateralis, are inserted into the suprarostrale[1], which—unlike the superior labial cartilage[1] of *Xenopus*—is moveable.

The Intermandibularis separates into the Intermandibularis anterior, Mandibulo-labialis, and Intermandibularis posterior.

The Levator hyoidei separates into the Orbito-hyoideus, Suspensorio-hyoideus, and the Hyo-, Suspensorio-, and Quadrato-angularis.

The Interhyoideus is a simple band, as in *Xenopus*.

It may be concluded that whilst the horizontal position of the palato-quadrate, the forward migration of Meckel's cartilage and of the hyobranchial skeleton, the horizontal position of the masticatory muscles, and the forward migration of the hyobranchial musculature, are the result of the elongation of the intestine; yet the insertions of the Levatores mandibulae posterior sublimis, subexternus and lateralis into the suprarostrale, the formation of the Mandibulo-labialis, and the subdivision of the Levator hyoidei—phenomena, all of which disappear at metamorphosis—are due to another, additional, cause—the development of a ventral suctorial mouth with horny jaws and a small Meckel's cartilage.

Larvae of *Xenopus* show the result of only one factor—the elongation of the intestine. Larvae of *Anura phaneroglossa* show that of two factors—the elongation of the intestine, and the development of a suctorial mouth.

I am indebted to Miss Cross for the drawings of the model, and to Mr Emery for help in making it.

ABBREVIATIONS IN FIGURES

ann. tymp.	annulus tympanicus	*Lev. mand. post.*	Levator mandibulae posterior
asc. proc.	ascending process of palatoquadrate	*Meck. cart.*	Meckel's cartilage
		musc. proc.	muscle process of palato-quadrate
aud. caps.	auditory capsule		
basihyobr.	basihyobranchiale	*pal. proc.*	palatal process of palato-quadrate
Interhy.	Interhyoideus		
Intermand.	Intermandibularis	*palquad.*	palatoquadrate
Lev. hy.	Levator hyoidei	*sup. lab. c.*	superior labial cartilage
Lev. mand. ant.	Levator mandibulae anterior	*tegmen tymp.*	tegmen tympani

[1] It does not appear certain that these two cartilages are homologous.

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COMPLETE DOUBLE AORTIC ARCH

By ROBERT D. LOCKHART, Ch.M.
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This specimen was removed from a dissecting room subject, a man of 67 years.

The ascending aorta divides into right and left arches which fuse to form the descending aorta after enclosing the trachea, oesophagus, and thoracic duct in an arterial collar, without undue pressure upon the transmitted structures. The vagus and recurrent nerves are related to the lateral and medial sides respectively of their own arches. The common carotid artery and the subclavian artery arise symmetrically upon each arch and the branches of each subclavian are the vertebral, thyreoid axis, superior intercostal and internal mammary arteries.

While the literature contains some nineteen references (1–19) the cases are mostly children dying within seven months after birth, exhibiting stridor, cyanosis, dysphagia, and pulmonary infection. Very few instances, indeed, have been described in adults, and in these one or other arch is usually represented by a fibrous strand, or is barely pervious, but the occurrence of such a completely formed fully functioning pair of arches of definitely satisfactory calibre, comparable to the present case, is exceedingly rare.

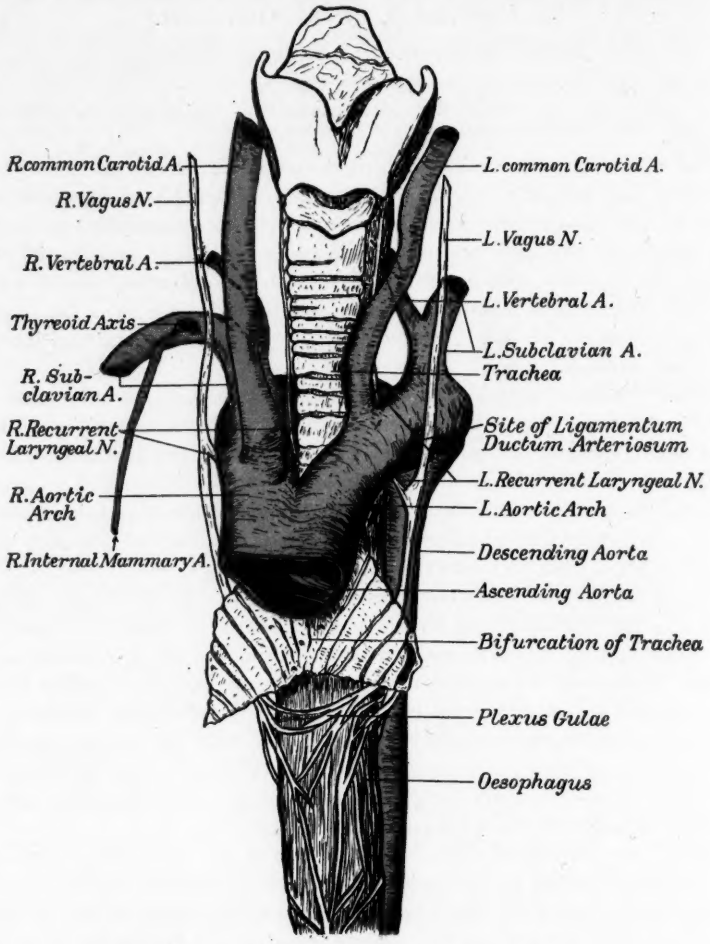
The arrangement of the structures in cases of double aortic arch is usually similar to the accompanying illustrations, although, in Malacarne's case, the pulmonary artery also traversed the arterial ring, while, in Zagorsky's, the trachea alone was transmitted. Malacarne's case was also peculiar in that the origin of the vessels from each arch, namely subclavian, external and internal carotid arteries cannot be reconciled with the known modes of development of the vascular arches (20). In Watson's case the vertebral arteries arose directly from the arches, and in this one it will be seen that the vertebral arises from the subclavian close to the arch.

The whole interest of such a specimen lies in the fact that it stands as a milestone of striking and historic architecture upon the byways of development, and the reason for its persistence is to be explained by the same delicate decisions that account for the maintenance or the discarding of its contemporaries, with the presence in this instance of some defective bias in the finely jewelled movements of early embryonic rhythm, defective, that is, for the production of the standard pattern.

It is true that the double arch is typical of the reptilian type, that the left arch disappears in birds and the right arch in mammals. While the arches of this individual have taken their stand at the reptilian cross-roads, opinion

is averse to considering such aortic anomalies in man as an atavistic tendency (21–23).

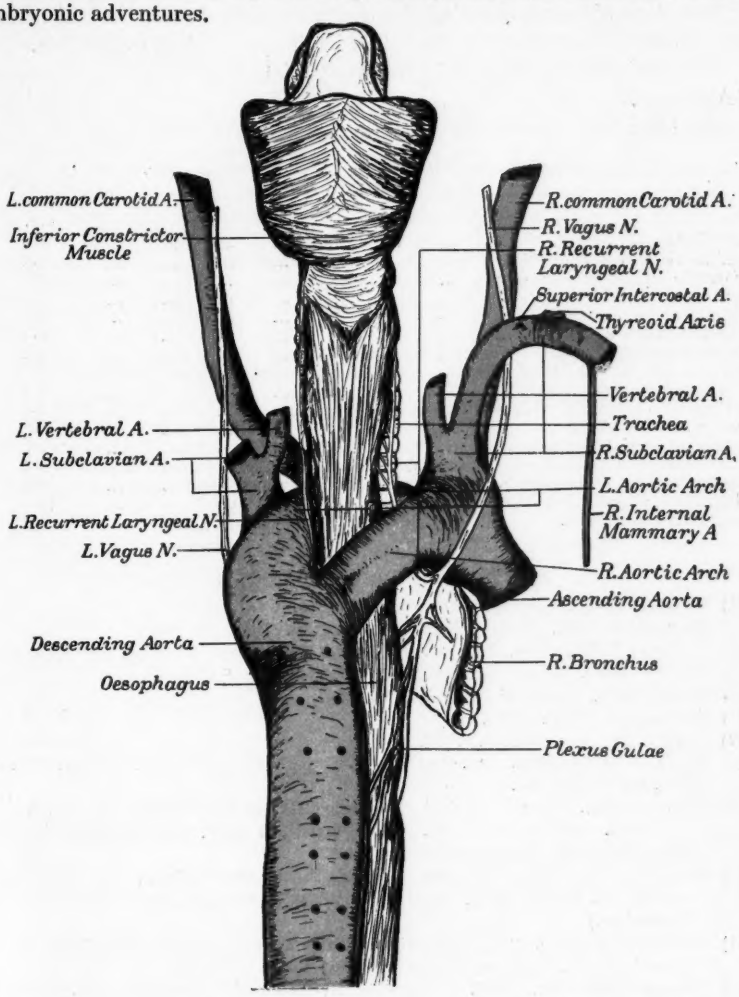
The early embryonic arches are really anastomosing arterial networks (24), and we are inclined to think that the whole question of the persistence or



Double aortic arch, anterior aspect. Half natural size.

disappearance of these networks is purely mechanical, that the selection of one anastomosing arterial network for exploitation into a permanent arterial highway is the result of, say, some slight gravitation, some growing tissue spur, that plays the part of a tiny watershed amid the microscopic mountains

of the second week embryo, with the resulting disuse of other arches and their consequent obliteration. The wonder is that the so-called normal arrangement is produced with such uncanny similarity so frequently, amid such hair's-breadth embryonic adventures.



Double aortic arch, posterior aspect. Half natural size.

Whatever the exquisite nature of the developmental interaction, it appears that Nature seldom indulges in the dangerous experiment of transmitting man's trachea and oesophagus through an arterial collar with any measure of success for more than a few months after birth.

The subject showed no other noteworthy features save engorgement of the veins of the head and face. The occipital vein almost vied with a normal internal jugular vein.

The diagnosis accompanying the case was that of morbus cordis. There may not be so much security after all in having two strings to the bow.

The specimen is preserved in the Anatomical Museum of the University of Aberdeen.

The following measurements have been made.

Ascending aorta bifurcates 8 cm. from the aortic valve.

	External circumference cm.
Ascending aorta	9·0
Right aortic arch at bifurcation	5·5
Left aortic arch at bifurcation	6·3
Right arch at fusion	5·0
Left arch at fusion	7·4
Descending aorta at origin	8·0
Left arch at site of ligamentum ductum arteriosum	7·6
Left arch just beyond site of ligamentum ductum arteriosum where crossed by the vagus nerve	7·4
Left arch just before site of ligamentum ductum arteriosum	6·5
Trachea at cricoid level	7·9
Trachea at arterial ring	6·7
Widest transverse width of oesophagus, just below cricoid, external measurement	2·6
Transverse width of oesophagus at arterial ring, external measurement	2·3
Arterial ring, internal circumference	10·4

Heart valves competent.

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SOME NOTES ON THE EARLY ADRENALS[1]

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In the adrenal of a new-born baby, the cortex consists of two layers, namely, an outer thin zone of tissue that is mainly basophilic in staining character, and an inner zone of greater width that is mainly eosinophilic. Because of these staining qualities the outer zone has a bluish tinge when stained by haemotoxylin and eosin, and the inner zone, when similarly stained, is of a pink colour. The outer zone is called the "adult cortex," and the inner zone is called the "foetal cortex."

In 1911 Armour and Elliott drew attention to these two layers in the adrenal cortex of the new-born babe, and noticed that soon after birth the adult cortex begins to grow, while the foetal cortex begins to degenerate. In 1926 Lewis and Pappenheimer expressed the belief that these post-natal changes were in no way altered even if the child were born prematurely. In 1927 Lucas, Keene and Hewer reported that the foetal cortex has begun to degenerate even during the last ten weeks of intra-uterine life.

METHOD

Adrenals were obtained at autopsies from foetuses and infants. Autopsy was performed usually within 12 hours of death. The tissue was fixed in 10 per cent. formalin, and stained with haemotoxylin and eosin. In addition, Van Gieson and Scharlach R. stains were used on many sections. Some of the slides were obtained from amongst those kept on file at the Mayo Clinic since 1923. All the Van Gieson stained slides were made from the paraffin blocks kept on file since 1923. In some cases slides were stained by the methods of Nissl and Orlandi, from the original paraffin blocks. In addition I had permission to examine slides retained in Dr Adair's department at the University of Minnesota.

HISTOLOGICAL CHANGES

In about 10 days after birth a change is seen to take place in both the adult and foetal cortex of the adrenals. The foetal cortex is seen to be replaced slowly by adult cortex. The adult cortex consists of cells whose nuclei are

[1] Work done at the Mayo Clinic, Rochester, U.S.A.

smaller and whose cytoplasm is less abundant than the nuclei and cytoplasm of the cells in the foetal cortex. The arrangement of the cells in the two layers is different, those in the adult cortex tending to form clusters like bunches of grapes. When stained by haemotoxylin and eosin both the cytoplasm and the nuclei of the cells of the adult cortex seemed to stain more deeply than those in the foetal cortex. Various other stains were used, but did not reveal any additional changes. In Table I are shown the relative thickness of the zones of adult and foetal cortex. The ratio has a mean value of about 0·25 at term, but in case numbers 12, 16, 20, and 21 post-natal development has raised the ratio to above unity. See figs. 1 and 2.

The adult cortex seems to make its first appearance at about the middle of the 7th month of intra-uterine life. The adrenals from a still-born infant of 6 months gestation showed no adult cortex, but seemed to consist entirely of foetal cortex. The adult cortex grows only for a short period in the last 6 weeks of intra-uterine life, and then discontinues its growth, so that the relative depth of the adult cortex is the same in full-term infants as in infants of less than 6 weeks prematurity. Within 10 days of birth there are distinct signs that definite growth has recommenced in the adult cortex.

ANENCEPHALY

Many writers have drawn attention to the apparent maldevelopment of the adrenals in cases of anencephaly. I have had the opportunity of studying the autopsy reports of a group of anencephalic monsters, and of studying the microscopic slides of some of the adrenals. In several of these cases the adrenals are markedly under weight, as shown in Table II. However there were two cases in which the adrenals were of normal weight. The microscopic slides for these were unsatisfactory. I append more detailed protocols of these two cases. Of the entire group of anencephalic monsters, the microscopic slides were unsatisfactory in all except three cases, because post-mortem degeneration and haemorrhage had evidently been present before sections were taken. In three new-born anencephalic monsters, in which cases the microscopic slides were satisfactory, the adult cortex had developed to such a degree as that usually shown by the normal babe at the end of the 3rd week of post-natal life. Evidently this seemingly precocious development took place *in utero*. Scammon and Nañagas have shown that anencephalic monsters are not the subjects of generalised underdevelopment, but that some parts of the body, such as the upper limbs, undergo excessive and precocious growth.

The question arises as to whether there is a parallelism between the maldevelopment of the brain and the maldevelopment of the adrenals. I examined the autopsy reports, and the microscopic slides of the adrenals, in a number of cases of hydrocephalus, in which the brain showed signs of pressure atrophy: but the adrenals seemed normal in size and structure. (See Table III.)

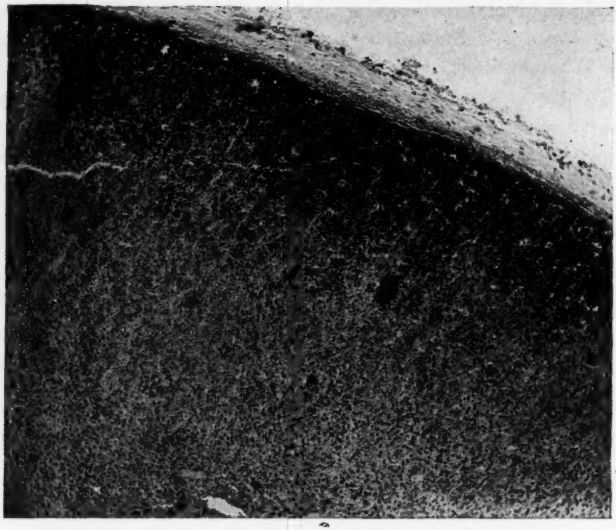

Fig. 1. Adrenal of stillborn babe, showing narrow outer zone of adult cortex. (× 50.)

Fig. 2. Adrenal of babe aged 2 weeks showing band of adult cortex of greater depth than at birth (Fig. 1). (× 50.)

CONCLUSIONS

In 18 premature and normal new-born babes the ratio of the thickness of the adult to the foetal cortex has been found to be about 0·25. In four cases ranging in age from 15 days to 61 days the ratio is shown to have increased from 1 to 3.

The cortex of the suprarenal in the premature child develops in a normal manner as though it were not premature. The rate of growth of the adult cortex and of disappearance of the foetal cortex may be used as a rough estimate of post-natal age.

There are apparently some cases of anencephaly, in which the adrenals are of normal weight; and some cases of anencephaly in which the adult cortex of the adrenals undergoes precocious development *in utero*.

In a group of cases of hydrocephalus associated with brain atrophy, the adrenals seemed normal in size and structure.

APPENDIX

TWO CASES OF ANENCEPHALY WITH NORMAL ADRENALS

Case 1. Female child of white parentage, 8 months gestation, weighing 1800 gm. The eyes are exophthalmic in character. There is marked congestion and cyanosis of the conjunctivae. There is malformation of the head. The scalp, calvarium, dura and dural sinuses are missing. The supra-orbital ridges are prominent. The base of the skull is covered with a reddish granulation-like tissue, but no definite structure can be made out. The fossae of the skull are flattened and there is absence of development of the medulla and cerebellum. The neural arches of the upper six cervical vertebrae have failed to fuse, and there is a triangular shaped deficiency on the dorsum of the neck which is continuous with the defect in the skull. The cervical portion of the spinal cord is poorly developed, but a few nerves in the upper portion can be made out. The remainder of the spinal cord shows no evidence of haemorrhage or trauma. The right adrenal weighs 4·3 gm., and the left 5·6 gm. They are normal in position. The surfaces are congested, and on section the centres are reddish brown in colour.

Case 2. A female weighing 2000 gm. There is absence of the scalp and calvarium, the outer surface of the cranial mass being composed of meninges. On opening this membrane, the tissue underneath is composed of soft reddish material. There is no evidence of any development of the cerebrum or cerebellum. The pituitary is apparently normal: and a few cranial nerves can be made out. There is marked exophthalmos and congestion of the mucous membrane. The adrenals seem to be normal.

Table I. *The Foetal and Neo-Natal Suprarenal Cortex.*

Case No.	Foetal age in months	Extra-maternal age	Adult cortex Depth in mm.	Foetal cortex depth in mm.	Ratio of adult cortex / foetal cortex
1	5·5	1 hour	0·3	1·3	0·23
2	6·0	—	0·3	1·3	0·23
3	6·0	6 hours	0·3	1·35	0·22
4	5·5	—	0·25	1·25	0·2
5	6·5	—	0·3	1·0	0·3
6	6·5	—	0·35	1·5	0·23
7	6·5	—	0·3	1·7	0·17
8	6·5	2 days	0·25	0·95	0·25
9	6·5	—	0·3	1·15	0·26
10	6·0	7 days	0·4	1·1	0·36
11	7·0	—	0·25	1·25	0·2
12	7·0	3 weeks	0·6	0·6	1·0
13	7·0	6 hours	0·3	1·0	0·3
14	8·0	17 hours	0·25	1·4	0·17
15	8·0	—	0·2	1·3	0·15
16	8·0	15 days	0·55	0·35	1·5
17	8·5	—	0·3	1·4	0·21
18	9·0	—	0·12	1·5	0·08
19	9·2	—	0·1	2·2	0·04
20	9·0	20 days	0·85	0·5	1·7
21	9·0	2 months and 11 days	0·6	0·2	3·0
22	6·0	—	0·25	0·9	0·27

Table II. *The Suprarenals in Anencephaly.*

Case No.	Weight of Adrenals in gmm. Right adrenal	Left adrenal	Total weight	Pertinent autopsy findings
1	0·8	0·5	1·3	Gestation was 8 months: anencephaly: craniorhachischiscis: congenital absence of left kidney, pelvis, and ureter.
2	1·0	1·0	2·0	Gestation was 8 months: anencephaly.
3	0·5	0·4	0·9	Gestation was 7·5 months: anencephaly: craniorhachischiscis.
4	1·4	1·8	3·2	Full term infant: anencephaly: craniorhachischiscis.
5	2·0	1·5	3·5	Anencephaly: craniorhachischiscis.
6	1·0	1·0	2·0	Gestation was 8 months: anencephaly: craniorhachischiscis.
7	0·6	0·6	1·2	Anencephaly: craniorhachischiscis

Table III. *The Suprarenals in Hydrocephalus.*

Case No.	Adrenal weight in gmm. Right	Left	Total weight	Gestation	Greatest circumference of head in cm.	Remarks
1	3·8	3·8	7·6	Term	39	Stillborn
2	4·0	3·5	7·5	„	—	Head is markedly hydrocephalic. Antepartum death
3	4·5	4·0	8·5	„	38	Stillborn
4	4·0	3·5	7·5	„	43	Died a few minutes after birth
5	2·5	3·0	5·5	„	41	Died one hour after birth
6	4·0	3·5	7·5	„	36	Stillborn
7	2·0	2·0	4·0	„	39	Stillborn
8	Adrenals are fused		5·0	„	—	Hydrocephalus, horseshoe kidney

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OBSERVATIONS ON THE MESENTERIC CIRCULATION

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In this article are submitted certain observations on the mesenteric circulation, which are based on a research carried out at the Pathological Institute of the London Hospital and in the Anatomical Department of St Mary's Hospital. In this research a large number of post-mortem and dissection bodies were examined to study the arrangement and distribution of the mesenteric vessels, and numerous experiments were performed with the object of investigating the collateral circulation in the territory of these vessels.

THE ARRANGEMENT AND DISTRIBUTION OF THE MESENTERIC VESSELS

These were studied in a large number of specially injected specimens, and were found to differ from accepted descriptions in the following particulars:

(1) The first of these deals with the *vasa recta*, or straight vessels, which pass from the terminal row of arcades to the gut-wall, on which they ramify. Measurements showed that in the upper jejunum they are fully $1\frac{1}{2}$ in. long, but they gradually become shorter, as the gut is traced downwards, until, in the lower part of the ileum, they measure less than $\frac{1}{2}$ in. in length. They are thin vessels which pursue an absolutely straight course until they reach within $\frac{1}{4}$ in. of the intestine. The accepted teaching, based on publications by French anatomists, is that at this point the vasa divide into two branches, which pass on opposite sides of the mesenteric border and encircle the gut.

The writer's investigation leads him to the conclusion that this teaching is absolutely inaccurate. A number of injected specimens was examined for this purpose, and it was proved, to the writer's satisfaction, firstly, that the vasa in most cases do not divide until they actually reach the gut-wall, and, secondly, that when they do divide early, both branches usually pass on the same side of the intestine (see fig. 1). Actually, the vasa curve slightly as they reach the gut-wall and pass onto one or other side of it, raising, as they do so, a thin fold of peritoneum away from the general level of the mesenteric attachment. Roughly speaking, the vasa pass alternately to one or other side of the intestine, but the writer cannot agree with G. M. Monks (quoted by Moynihan[1]) that this arrangement is invariable. Sometimes groups of four or five adjacent vasa were seen all passing to the same side of the gut.

[1] *Abdominal Operations*, Moynihan, 1914.

On the wall of the small intestine the vasa ramify in an arborescent manner, producing, in injected specimens, a really beautiful picture. In spite of this rich arborescence, however, there is absolutely no evidence that the branches of contiguous vasa anastomose. This subperitoneal ramification stops short a little distance from the antimesenteric border of the gut, which, in all the injected specimens, was presented as a clear longitudinal band, completely free from visible vessels. On the wall of the colon the ramification is not arborescent, but looks rather like bunches of very fine coiled hair.

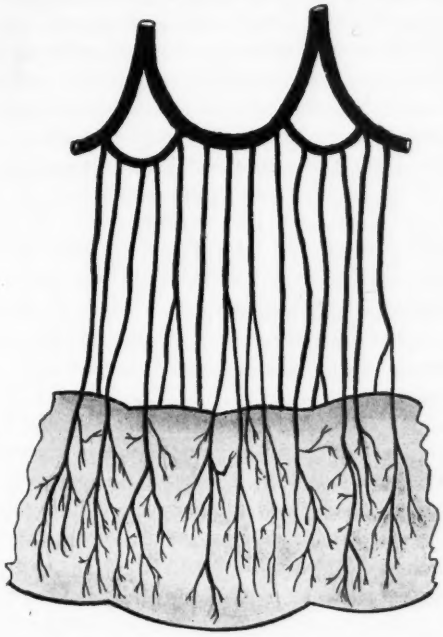

Fig. 1

(2) The second observation deals with the *venous drainage of the intestine.* The arrangement of the mesenteric veins was found to be much less constant than that of the arteries. The arrangement of the venous arcades and vasa recta was found to correspond very closely with that of the corresponding arteries, but more centrally several discrepancies were observed. The following are the most important:

(*a*) The jejunal and ileal veins were found more variable in number than the arteries. Thus, in one case only seven veins were counted actually opening into the superior mesenteric, while there were thirteen branches arising from the corresponding artery.

(*b*) Many variations were found in the manner of termination of some of

the main venous tributaries. Thus, in two out of twelve bodies in which the veins were specifically injected, the middle colic vein opened directly into the portal vein, while in two others the inferior mesenteric opened into the superior mesenteric, instead of the splenic.

(*c*) The most striking disparity, however, was observed in connection with the veins of the ileo-caecal region, and it was on this point that the arrangement was found to disagree entirely with accepted teaching. In four standard anatomical text-books which were consulted the ileo-caecal region is described as being drained by radicles which join to form an "ileo-colic vein," which is said to accompany the ileo-colic artery, and open into the superior mesenteric vein a good way up the root of the mesentery. In the great majority of the twelve bodies mentioned above, however, the venous radicles draining this region were found *not* to constitute by their junction an ileo-colic vein, but to form instead the commencement of the superior mesenteric vein itself. In most of these cases a small vein was certainly seen accompanying the ileo-colic artery, but it proved to be merely an anastomotic communication between the superior mesenteric vein and the marginal arcade along the ascending colon, and certainly not a functional ileo-colic vein.

(3) The third observation deals with the *blood-supply of the great omentum*, which was investigated at the suggestion of Prof. J. E. S. Frazer. This has been a matter of considerable difference of opinion, but the current view seems to be that the omentum is supplied by both the gastro-epiploic and the colic vessels. In this series of experiments the middle colic artery or vein was injected in ten bodies. In nine of these no trace of indian ink, the injection material, was found in the omentum; in the tenth, one injected vein was traced into this structure, but, as pathological adhesions were present in the immediate neighbourhood, they were probably responsible for the presence of this vessel. On the other hand, the gastro-epiploic vessels were injected in several cases, and invariably numerous injected vessels were traced into the omentum. In a number of bodies in which both the gastro-epiploic and middle colic veins were injected, a striking thing was observed—viz. that while the veins in the anterior double layer of the omentum, running down from the gastro-epiploic, showed the injection beautifully, the posterior double layer, which is attached to the transverse colon, and in which the tributaries of the middle colic would presumably run, did not show the injection at all.

One may safely conclude that the omentum normally receives its supply from the gastro-epiploic vessels. The writer has since been informed by Prof. J. E. S. Frazer that he came to the same conclusion on purely embryological grounds.

THE COLLATERAL CIRCULATION IN THE MESENTERY

The major part of this research deals with the collateral circulation in the territory of the mesenteric vessels. The experiments were carried out with two objects in view: (1) to work out, as far as possible, the degree of collateral

arterial supply and venous drainage in the mesenteric circulation; (2) to study the anatomical effect of experimental occlusion of the main vessels and of various branches.

Experimental work by Litten in 1875 (quoted by Trotter[1]) led him to the conclusion that the mesenteric arteries and their main branches behaved physiologically as end-arteries, and that the rich anastomosis provided by the mesenteric arcades was functionally negligible. In spite of some opposition (Lagane[2]) this view has been very generally accepted by the surgical world, as, at first sight, it seems to correspond with the results of pathological and traumatic occlusion of the vessels.

On logical grounds, the writer found it difficult to accept this view, and decided to investigate the matter by ligature and injection experiments. The subjects were all post-mortem bodies, and to balance the loss of peripheral resistance in the cadaver, the injections were all made at pressures much below the normal blood-pressure. The material used was a 1 in 5 solution of indian ink, which proved very satisfactory, as it picked out the very finest twigs in the mesentery and on the gut-wall.

The experiments fall into three groups:

(1) In the first group various vessels were ligatured and a proximal injection was made into the main trunk, behind the ligature, with the following results:

Ligature of the *jejunal and ileal rami*, singly or in contiguous groups of two and even three, in no case prevented the injection material reaching the entire territory of the occluded vessels by collateral channels, although the injection was made at a pressure of only 20 mm. Hg (fig. 2).

Ligature of vessels running from proximal to more distal arcades had precisely the same negative result.

Ligature of a *terminal arcade* in two places, however, completely obstructed the flow of ink to the vasa arising between the ligatures and to the gut supplied by them, although the injections were made at pressures up to 100 mm. Hg. The sharp margin between the injected and non-injected gut and mesentery was very striking (fig. 3).

Ligature of the *vasa recta* themselves had the same result.

Ligature of the *ileo-colic artery* produced results which varied with the pressure of the injection. At 80 mm. Hg the injection reached the entire distribution of the occluded vessel.

Ligature of the *right colic* failed to obstruct an injection at 40 mm. Hg, which reached the entire ascending colon and hepatic flexure by collateral channels.

Lastly, the *superior mesenteric artery and vein* were ligatured at various levels and proximal injections made at various pressures, but a description of one of these experiments is all that space will permit. In this the superior mesenteric artery was ligatured below the origin of its middle colic and upper two jejunal branches, and an injection made above the ligature at 80 mm. Hg.

[1] *Embolism and Thrombosis of the Mesenteric Vessels*, L. B. C. Trotter, 1913.
[2] *Thèse de Paris*, Lagane, 1911.

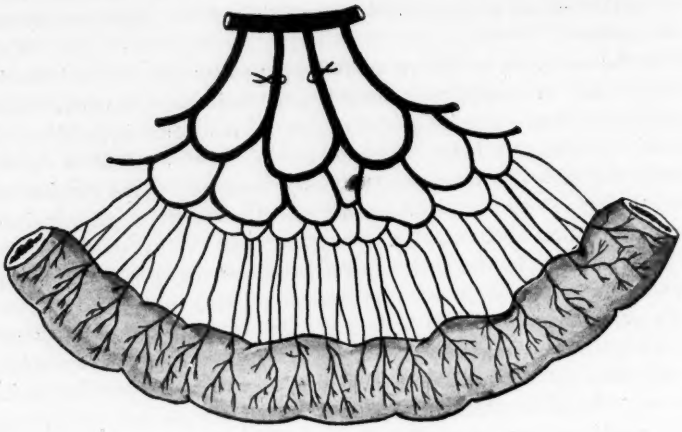

Fig. 2

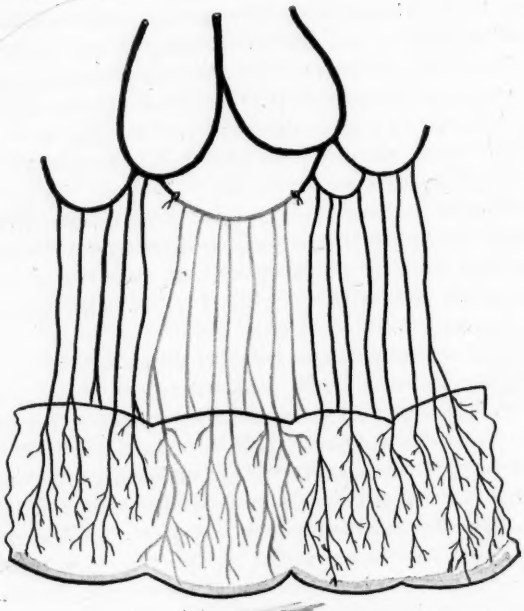

Fig. 3

The lower four rami only and the corresponding gut failed to take the injection, the ink spreading along the mesenteric arcades to the seventh ramus, and along the paracolic arcades to the caecum and terminal part of the ileum.

(2) In the second group of experiments an attempt was made to determine the potential area of supply, and, therefore, the collateral overlap, of branches of the main vessels.

In one experiment an ileal ramus was injected at 20 mm. Hg and the ink showed up in 5 ft. of intestine, representing a collateral overlap of nearly 300 per cent.

In another experiment the fourth jejunal ramus was injected at 80 mm. Hg and the ink reached the upper two-thirds of the small intestine, showing an overlap of over 700 per cent.

Many experiments of this type were performed with very similar results.

(3) The third and last group of experiments was made to investigate the functional value of the external anastomoses of the mesenteric vessels.

The superior mesenteric artery was ligatured above the origin of its branches and attempts were made to inject its territory from collateral channels, such as the gastro-duodenal, inferior mesenteric, last dorsal and lumbar arteries. Only injections made at pressures above the normal systolic pressure penetrated into any considerable part of the occluded territory.

The *conclusions* arrived at from this research can be summarised as follows:

(1) The collateral circulation within the mesentery itself, up to and including the terminal row of arcades, is very free, and occlusion of quite large vessels fails to prevent injections at fractional pressures reaching every part of their territory.

(2) The collateral circulation stops with the terminal row of arcades. Beyond this there is absolutely no anastomosis, either between the vasa recta in the mesentery, or between the ramifying vessels on the gut-wall. One fears that the last observation contradicts the view of many authorities, but its accuracy is guaranteed.

(3) The external anastomoses of the mesenteric vessels are as inefficient as their anatomical construction would lead us to expect.

In this sense only is the mesenteric artery an end-artery.

An opportunity was sought to test these conclusions by an extensive clinical and pathological research on morbid occlusion of the mesenteric vessels. Without entering into a description of the results obtained, the writer would like to conclude by stating that these results confirmed the above observations in every particular, and that the infarction of the intestine which so often follows traumatic and pathological occlusion within the mesenteric territory is not due to failure of the collateral circulation, but to secondary changes in the mesentery, and to a thrombosis spreading peripherally from the point of occlusion, through the mesenteric arcades, to the vasa recta and the gut itself.

ABNORMALITIES OF THE VERTEBRAL COLUMN IN A SERIES OF SKELETONS OF BANTU NATIVES OF SOUTH AFRICA

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IX.	Malformation of the body of a thoracic vertebra	225
X.	Abnormality of the lumbar transverse processes	227
XI.	Abnormality of the twelfth thoracic vertebra	228
XII.	Congenital division of the vertebral lamina	228
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I. INTRODUCTION

The Anthropological Museum of the Anatomy Department of the University of the Witwatersrand contains the skeletons, classified as to age, race and sex, of some 80 natives of the Bantu races of South Africa.

A systematic examination of this material has revealed, among other interesting features, certain abnormalities of the vertebral column which form the basis for this article.

The available material is small in comparison with that furnished by such anthropological collections as that of the Western Reserve University, Ohio, but it must be remembered that the systematic collection of anthropological material, with information as to age, race, sex and other data, has made little more than a beginning in South Africa.

No apology, however, is needed for presenting a paper based on material which, though relatively scanty, is the result of methodical collection, and is probably the chief material of its type available in South Africa for the study of the comparative osteology of the Bantu.

My general anatomical experience in London soon showed me, on examining this material in Johannesburg, that abnormalities are more common in the vertebral columns of the Bantu than in those of the European. The skeleton of the Bantu may be briefly described as more plastic and less rigid in its design than that of the European.

The studies of Wingate Todd (1) on the vertebral column of Mammalia, in which he reviews the "modal" number of thoracico-lumbar vertebrae in the mammalian orders from the evolutionary standpoint, have afforded illuminating suggestions for the interpretation of certain abnormalities found in the vertebral column of man.

The more detailed work of Willis on the stability of the vertebral column of man (2), and especially on the lumbo-sacral region (3), on a material that includes 748 columns have been utilised as data of comparison between the white and negro races of America on the one hand, and the Bantu races on the other.

Anthropological work on the native races of South Africa has been for the most part confined to anthropometric studies. While most important observations and inferences have been made, these studies have nevertheless been based on collections which are small and, for the most part, widely separated. Thomson (5), in a study of three Bushman skeletons only, has contributed a series of measurements with estimation of indices and some deductions as to the curves of the vertebral columns. Anthropometric observations on the whole skeleton are to be found in the student's guide written by Prof. Drennan of Capetown (6), but are based on a less extensive material than that available to me. The writings of Shrubsall (7) on the Strandlooper, and of Broom (8) on the cranial characters of the Bushman and the Hottentot also represent conspicuous additions to our knowledge of the South African peoples.

Invaluable as these studies are, it must be said that no comprehensive study of the abnormalities of the Bantu skeleton in an extended series of specimens has been produced hitherto, and I hope that this paper will assist in the study of the comparative anatomy of the Bantu before racial admixture renders such a task nugatory.

II. MATERIAL

Eighty-two vertebral columns have formed the material from which the examples of abnormality set out in the following pages have been collected. These skeletons include those of 17 females, 63 males and 2 of which the sex is not determined. The ages range from 15 to 90 years.

The Bantu skeletons in the Anthropological Museum of the Anatomy Department have been prepared from subjects received for the ordinary purposes of an Anatomy School. All skeletons of individuals of known mixed

race, such as those of the "coloured" Eurafrican hybrid, and all skeletons of Asiatics have been excluded from this survey in an attempt to collect material which is, in a racial sense, homogeneous. As no selection is exercised, the material should be quite representative of the Bantu native race. The occasional inclusion of a skeleton to which the only description is "Kaffir of unknown tribe" must be admitted.

The vertebral columns have not always been complete in every detail; occasionally vertebrae have been lost during the preparation of the skeleton. The actual numbers of specimens of each vertebra examined are given below:

Cervical	I	II	III	IV	V	VI	VII					
	79	80	77	79	80	81	82					
Thoracic	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
	82	82	81	81	82	82	82	80	80	80	81	81
Lumbar	I	II	III	IV	V							
	82	82	80	82	81							

In all 1936 vertebrae and 81 sacra have been examined for abnormality. The definition of abnormality is not easy, but the following considerations have determined whether a vertebra or a column has been deemed normal or not. Any feature of a vertebral column, in respect of which it departs from the arrangement accepted by common usage as the normal of man, or any feature of a vertebra, by virtue of which it lacks symmetry or harmony with its neighbours, has led to the inclusion of the column or of the vertebra in the material on which these notes are based. To this must be added the reservation that there must be absence of any circumstances that suggest that disharmony or asymmetry may be the result of pathological processes.

In all 77 abnormal vertebrae were collected from 82 columns.

In the schedule of abnormalities which follows 82 examples of abnormality are shown. In a few instances a vertebra has received consideration in two different places; for example, a first sacral vertebra which exhibits spina bifida as well as separation from the sacrum is considered in both Section VI and Section IV B.

Schedule of Morphological Abnormalities of the vertebral columns in the Anatomy Museum of the University of the Witwatersrand

Section	Examples	Museum numbers
IV. Abnormalities of the lumbo-sacral junction		
(A) Vertebrae of transitional form at the lumbo-sacral junction	4	179, 188, 253, 282
(B) Separation of the first sacral vertebra	7	178, 197, 217, 221, 241 A, 263, 309
V. The "six-piece" sacrum		
(A) Thirtieth vertebra of coccygeal type	6	193, 203, 220, 236, 247, 285
(B) Thirtieth vertebra of sacral type	10	188, 210, 221, 241 B, 252, 253, 280, 284, 303, 309
(C) Thirtieth vertebra of transitional form	1	311

Section		Examples	Museum numbers
VI.	Spina bifida	23	140, 157, 179, 188, 195 A, 205, 216, 232, 235, 236, 246, 284, 286, 307, 309
VII.	Absence of spinous processes	16	152, 157, 189, 195 A, 205, 246, 248, 284, 307
VIII.	Abnormalities of the sixth and seventh cervical vertebrae		
	(A) Cervical rib	2	239, 281
	(B) Reduction of the transverse process	2	159, 221
	(C) Absence of vertebrarterial foramen	1	159
IX.	Malformation of the body of a thoracic vertebra	1	262
X.	Abnormality of the lumbar transverse processes	2	332
XI.	Abnormality of the twelfth thoracic vertebra	1	307
XII.	Congenital division of the vertebral lamina	6	159, 248, 280, 303, 307
		Total 82	

III. THE DISTRIBUTION OF ABNORMAL VERTEBRAE IN THE VERTEBRAL COLUMN

Certain regions more commonly provide examples of abnormal vertebrae than others. This must be interpreted as an expression of instability of those particular regions of the vertebral column.

Graphic representation of the distribution of abnormal vertebrae

In fig. 1, the base line represents, space by space, the vertebrae enumerated from the head downwards, as the line is followed from left to right. Vertically is plotted in black, under its horizontal denomination, a square for each vertebra which presents features of abnormality. The same graphic value, i.e. one black square, has been given to each abnormal vertebra, and 77 abnormal vertebrae are represented in all.

The definition of abnormality proposed in Section II is a wide one. It might be supposed that a wide definition would be associated with a wide and, perhaps, an even "scattering" of abnormal vertebrae in the graph. On the contrary, fig. 1 shows that, despite the breadth of the definition, certain vertebrae are specially prone to abnormality. The first piece of the sacrum, the coccyx and, in a lesser degree, the upper and the lower members of each of the cervical, thoracic and lumbar series exhibit this tendency. It seems that the most variable vertebrae of all are the coccyx and the first sacral.

The graph shows that in the cervical and thoracic regions the middle members are the most stable. The same tendency in the lumbar region is less obvious, but is very striking in the sacrum. The regions most prone to variation are those in which vertebrae of one description meet those of another; that is, those regions where a transition of characters takes place in a normal column.

IV. ABNORMALITIES AT THE LUMBO-SACRAL JUNCTION

A glance at the graph, fig. 1, will show that the lumbo-sacral junction or, to be more precise, the first sacral vertebra, is one of the points in the vertebral column most liable to abnormality.

Abnormalities peculiar to this point include sacral vertebrae on which lumbar characters have been imposed, and lumbar vertebrae which bear sacral characters as well as intermediate or bizarre forms. In no part of the vertebral column, unless it be the caudal end of the sacrum, is the inherent

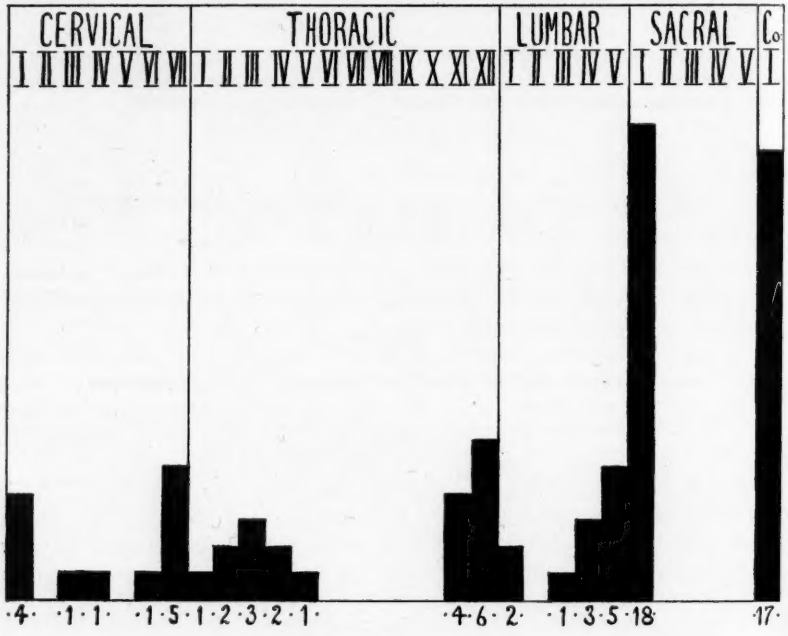

Fig. 1. This figure represents, in graphic form, the distribution of abnormal vertebrae in the vertebral column. The vertebrae are arranged, as from the head downwards, from left to right along the base line. Abnormal vertebrae are represented vertically below their designation. Each abnormal vertebra is represented by a black square.

variability of nature which lies at the root of the Darwinian conception of evolution more clearly exemplified in relation to human structure. To an observer of the human skeleton, the study of this region brings home the realisation that the accepted or common description of the vertebral column is, in truth, no more than the statement of an average. It is with vertebrae which demonstrate a departure from the average that this Section is concerned.

(A) *Vertebrae of transitional form at the lumbo-sacral junction*

Specimen 1. Fig. 2 is the right postero-lateral view of a "six-piece" sacrum (No. 179). The transverse process of the first unit is massive and, to a slight degree, bifurcate. The upper divisions of the transverse processes project laterally somewhat posteriorly to the plane of the lower divisions, which are much the stouter, and are both joined to the lateral alae of the sacrum by firm, bony union. The first vertebra of the sacrum, which also presents the condition of spina bifida, is the twenty-fourth member of an otherwise normal vertebral column, and does not enter into the sacro-iliac joint by its lateral processes. In view of these two circumstances the sacrum is considered abnormal only in respect of fusion of the fifth lumbar vertebra to it, the true sacrum being of normal proportions.

A bifurcate condition of the transverse processes, and the articulation of their lower divisions with the lateral alae of the sacrum is described by Sir Harold Stiles(9) among the variations of the fifth lumbar vertebra. In the case described here the promontory is on the twenty-fifth vertebra, or the true first sacral vertebra. The sacral features of the twenty-fourth vertebra are (1) increased bulk of the transverse processes, and (2) partial fusion with the sacrum.

Specimen 2. Fig. 3 represents a "six-piece" sacrum (No. 188), in which the first unit is the twenty-fifth vertebra. This vertebra is incompletely fused to the succeeding vertebrae, for the dorsal arch, the articular processes and the transverse processes remain in a separable condition.

The transverse processes exhibit the bifurcate character described in Specimen 1. The upper divisions project laterally as blunt prominences above and behind the lower divisions, which are in contact with but not fused with the lateral sacral alae. Symmetrical lines of cleavage, in continuation of the cleft between the first and second sacral vertebrae, can be traced between the lower parts of the transverse processes and the lateral sacral alae, and can be seen in fig. 3 to cut across the auricular surface. The twenty-fifth vertebra, therefore, enters into the sacro-iliac joint by its transverse process, though in a much smaller proportion than is usual.

Viewing the bone as a whole, the promontory seems to be on the second unit, i.e. the twenty-sixth vertebra, instead of the twenty-fifth, which is the normal condition. The following lumbar characters are exhibited by this twenty-fifth vertebra—(1) situation above the promontory, (2) bifurcate condition of the transverse process, (3) separable condition from the mass of the sacrum.

Regarding the twenty-fifth vertebra as sacral, the abnormal features are the following—(1) reduction of the normal share of S. I in the sacro-iliac joint, (2) separability from the mass of the sacrum, (3) characters which approximate to the lumbar type.

Sir Harold Stiles(9) refers to this condition also, and he figures a sacrum in which an almost identical condition is shown, using the term "sacralisation" of a lumbar vertebra. "Lumbarisation" of a sacral vertebra would be a term more appropriate to this particular specimen, because the abnormal vertebra is the twenty-fifth, and not the twenty-fourth.

Specimen 3. Fig. 4 shows a specimen (No. 253) in which the twenty-fifth vertebra is asymmetrical, being lumbar in type on the right side and sacral in type on the left side. On the right side the transverse process has the bifurcate form mentioned before, but its lower part does not make a contact with the right sacral ala. Part of the body and the whole of the dorsal arch are also separable from the sacrum. The left lateral ala of the sacrum is fused with the lateral element of the twenty-fifth vertebra, but no fusion line is perceptible.

On the left side the twenty-fifth vertebra enters into the sacro-iliac joint in the proportion usually borne by the first sacral vertebra. The right sacro-iliac joint

involves the lateral elements of 3 elements and the left joint of 4, though the lower limits of the joint areas are at the same level on both sides.

Fig. 2

Fig. 3

Fig. 2. This figure shows the twenty-fourth vertebra and the sacrum of skeleton No. 179 from the right and slightly from behind. It can be seen that the transverse process of the twenty-fourth vertebra is massive and bifurcate, and that the lower part is fused to the lateral mass of the sacrum. The line of fusion between the transverse process and the sacrum does not traverse the auricular surface, i.e. the twenty-fourth vertebra, though partly fused to the sacrum does not enter into the sacro-iliac articulation. It can also be seen that there is lack of fusion between the bodies of the twenty-fourth and the twenty-fifth vertebrae, and that the spinous process of the twenty-fourth vertebra is cleft in the mid-dorsal line. The hollow in the lateral mass opposite the second part of the sacrum, just posterior to the auricular surface, is an artefact.

Fig. 3. This figure shows the sacrum of skeleton No. 188 from the right lateral aspect, slightly from above. A cleft traverses the upper part of the auricular surface, showing the much reduced share of the twenty-fifth vertebra in the sacro-iliac articulation.

The whole sacrum is asymmetrical, even the body of the abnormal member bulks more on the left and, consequently, the promontory, which is on the abnormal member, is shifted slightly to the left. The anterior concavity of the sacrum is curved, as it were, on a smaller radius on the left than on the right side, and the lateral projection of the ala is also less on the left than on the right side.

As fig. 4 shows, the abnormal twenty-fifth vertebra is succeeded by 5 sacral vertebrae. The characters of this vertebra are so evenly divided between lumbar and sacral that it is difficult to give it a designation. This specimen must be regarded as an example of an incomplete reversion of the twenty-fifth vertebra to lumbar type. The incompleteness lies in the asymmetry, the left half only being completely sacralised.

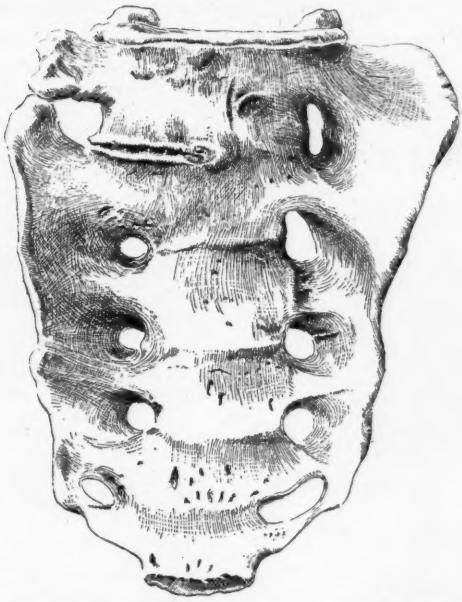

Fig. 4. This figure shows the anterior view of vertebrae 25 to 30 of skeleton No. 253. The left half of the twenty-fifth vertebra is of normal sacral form; the right half is of lumbar form and separate both as to body and transverse process from the twenty-sixth vertebra. The thirtieth vertebra is "sacralised."

Specimen 4. A more unusual specimen than the last was found in the skeleton of a male Marolong, aged 16 (No. 282), and is illustrated in a photograph, fig. 5. Again the twenty-fifth vertebra is asymmetrical, the right half being of lumbar and the left half of sacral type. In view of the age of the subject, the fact that fusion of the twenty-fifth and the next vertebra is incomplete is unimportant.

Two points of special interest are to be noted:

(1) The contact on the left side between the lateral processes of the twenty-fifth and twenty-sixth vertebrae, and between these and the ilium, is effected by a separate ossification. A wedge-shaped bone which enters into the left sacro-iliac joint can be seen in this position in both the anterior and the left lateral views shown in fig. 5.

(2) The thirtieth vertebra in this skeleton is a normal free coccyx. Therefore the sacrum retains its five-piece dimensions on the left side, but is reduced to 4 pieces on the right. A partial reversion on the part of the twenty-fifth vertebra to lumbar type has been effected without any attempt at compensation at the lower end of the sacrum. This is remarkable, because generally the human tendency to increase the sacrum to 6 units is much stronger than the tendency to reduce it to 4. A discussion on this point will be found in Section VII.

Discussion

Junji Toyoda (10) of Kyoto, in an account of vertebrae of transitional type found in the lumbo-sacral region of the Japanese, has reported 10 vertebrae of transitional type in 172 skeletons, a proportion equivalent to 5·8 per cent. of vertebral columns. The proportion of 4 such vertebrae found in 82 Bantu columns, if expressed as a percentage, has a value of about 4·8 per cent. The observations of other anatomists quoted by Toyoda show that the proportions of vertebrae of transitional type found in this situation vary from 1·3 per cent. to 18 per cent. The first estimate by Fretz (11) refers, I presume, to Europeans; the second, by Wetzel (12), to the Australian aboriginal.

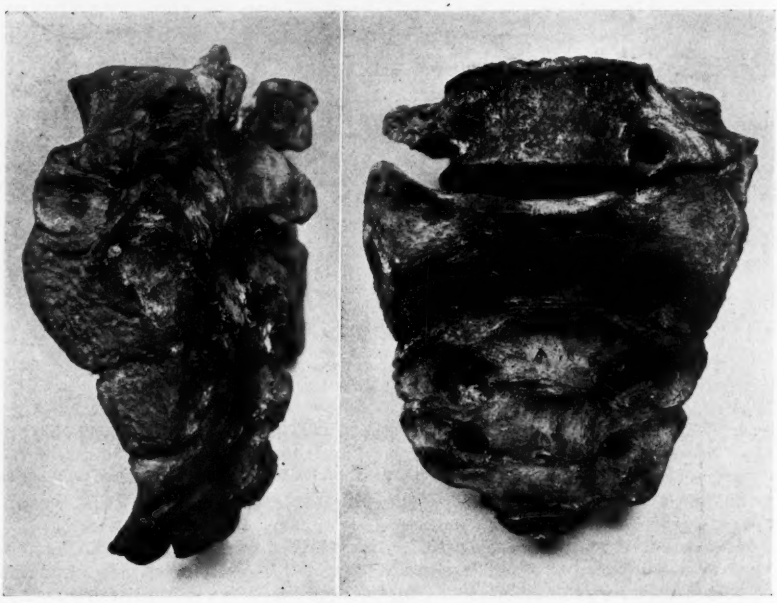

Fig. 5. This figure shows, on the left, the left side view and, on the right, the anterior view of the twenty-fifth and following vertebrae of skeleton No. 282. Note that the twenty-fifth vertebra presents lumbar characters on the right side and sacral characters on the left; the sacrum presents four-piece dimensions on the right side and five-piece on the left. A small wedge-shaped bone effects the contact between the lateral processes of the twenty-fifth and twenty-sixth vertebrae and the ilium, and can be readily seen in both views.

It seems that the positions of both the Japanese and the Bantu, as regards the frequency of occurrence of vertebrae of transitional type at the lumbo-sacral junction, are intermediate between that of the European and that of the Australian aboriginal.

In Toyoda's series of 10 the abnormal vertebra was usually asymmetrical

and incompletely fused to the sacrum. The twenty-fifth vertebra was the abnormal unit in 5 cases, the twenty-fourth in 4 and the twenty-third in 1 case. In 9 cases the abnormal vertebra constituted the first piece of a six-piece sacrum. In this Bantu series the abnormal vertebra is the twenty-fourth in 1 case and the twenty-fifth in 3 cases. In 3 cases the abnormal vertebra is part of a six-piece sacrum, and asymmetry is a feature of 2.

(B) *Separation of the first sacral vertebra.*

The phenomenon to be considered in this place is the separation of the first sacral or twenty-fifth vertebra from the main mass of the sacrum. In some specimens the only evidence of separation is seen in a cleft between the bodies of the first and second sacral vertebrae. Quain (13) refers to this condition as not uncommon in European skeletons. Such specimens, however, have not been included among those considered in this place, unless some other evidence of separation is also present, such as a cleft across the lateral sacral ala or a separable condition of the dorsal arch of the twenty-fifth vertebra. In all my specimens separation was evidenced by lack of fusion of the components of the dorsal arch; that is to say, the first sacral spine, the laminae and the articular processes of the twenty-fifth vertebra remained in a separable condition, and the joint cavities between the first and second sacral vertebrae were not obliterated. In 7 sacra the first vertebrae were partially separated. It is important to note that all these are from skeletons of full adults, whose ages range from 30 to 90 years. Two of these 7 sacra (Nos. 221 and 309) contain 6 vertebrae, and in both the thirtieth vertebra, which is incorporated in the sacrum, retains coccygeal form. This inclusion of the thirtieth vertebra in the sacrum suggests a measure of compensation for partial release of the twenty-fifth vertebra.

V. THE "SIX-PIECE" SACRUM

On theoretical grounds, the sacrum might be increased by the addition of a vertebra to either the cephalic or the caudal end. One example of addition to the cephalic end of the sacrum is afforded by Specimen 1 described in Section IV A. Increase of the sacrum by addition at the caudal end has proved to be the commoner condition.

In a normal column the thirtieth vertebra is the first piece of the coccyx. This vertebra may be incorporated into the sacrum in two ways and with two different results. In the one case the thirtieth vertebra assumes sacral characters, in the other case the thirtieth vertebra retains its coccygeal form though fused with the sacrum. These two varieties of "six-piece" sacrum present morphological features which are quite distinct from one another, and are recognisable at a glance. Fig. 6 shows both types; in the sacrum on the left the thirtieth vertebra retains coccygeal form, in the sacrum on the right the thirtieth vertebra is of sacral type. It is unfortunate that the skeletons

had not been prepared with a view to making possible a study of the coccyx, because the material is not available for me to discuss the condition of the coccygeal vertebrae in relation to the six-piece sacrum further.

(A) *Thirtieth vertebra of coccygeal type*

The drawing on the left in fig. 6 shows that the sixth piece of the sacrum is to a large extent separated from the fifth and other pieces by a deep notch on each lateral border. This open groove is the passage for the fifth sacral nerve, and, as the drawing shows, there is no fifth anterior sacral foramen. Because pathological processes leading to synostosis are of frequent occurrence in the vertebral columns of Bantu natives, specimens have been minutely scrutinised in order to separate examples of pathological synostosis from those of developmental fusion, with which this section is concerned. In any vertebral column in which the coccyx is fused to the sacrum, and in which evidence of pathological change of the sort referred to could

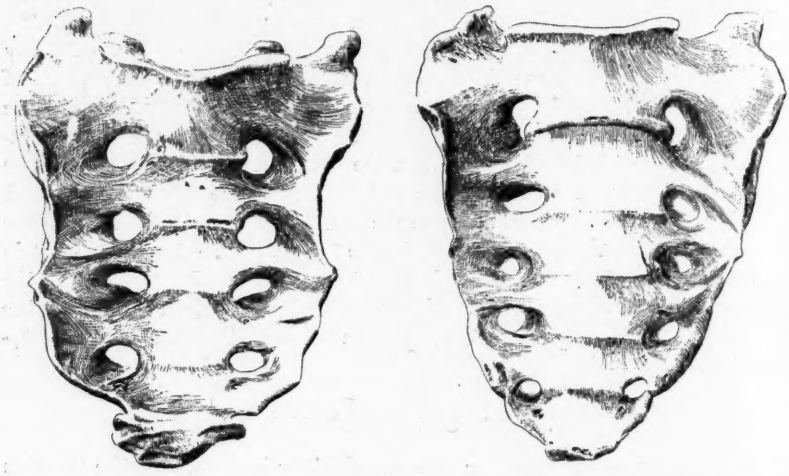

Fig. 6. This figure shows the anterior views of vertebrae 25 to 30 of two skeletons. The figure on the left shows that in No. 193 the thirtieth vertebra is fused to the sacrum, but has retained coccygeal form. In No. 284, on the right, the thirtieth vertebra is also fused to the sacrum but a fairly uniform curve joins the lower part of the auricular area to the tip of the thirtieth vertebra. In No. 284, the thirtieth vertebra is "sacralised."

be found, I have considered fusion to be pathological and not developmental in its nature. In only 6 out of 16 sacra, increased to 6 vertebrae by inclusion of the thirtieth, have I felt confident that the fusion was developmental and not pathological. It is possible and even probable that this estimate of the occurrence of developmental fusion of the thirtieth vertebra is too low. An individual with a fused coccyx might very possibly acquire, in later life, disease of the vertebral column of the nature suggested. Such a case would be excluded from its proper category by application of the reservation mentioned above.

(B) *Thirtieth vertebra of sacral type*

In contrast to the last, as the drawing on the right in fig. 6 shows, we may find a six-piece sacrum in which the lateral borders describe uninterrupted curves from below the lowest point of the auricular surface, i.e. from below the third sacral vertebra, to the lower borders of the sixth sacral vertebra. The passage for the fifth sacral nerve is completely surrounded by bone, that is to say, a fifth anterior sacral foramen is present. Then we may say the thirtieth vertebra has assumed sacral characters and is "sacralised."

This sacralisation of the thirtieth vertebra was found in 8 out of 81 sacra. To these may be added Specimens 2 and 3 described in Section IV A (Nos. 188 and 253). Now we have 10 examples of sacralisation of the thirtieth vertebra and 6 examples of fusion of the coccyx.

It is perhaps unexpected that examples of sacralisation of the thirtieth vertebra should be in numerical excess of examples of developmental fusion of that vertebra without modification of form. No great stress can be laid on the relative values of 10 and 6 in a short series, especially in view of a possible under-estimate of the occurrence of fusion of the coccyx.

(C) *Thirtieth vertebra of transitional form*

The thirtieth vertebra of skeleton No. 311 is fused to the sacrum but presents transitional characters; on the right side this vertebra is of sacral type, and on the left side of coccygeal type.

General comment on the abnormalities of the lumbo-sacral junction

It seems desirable at this point to review the abnormalities described in order to discover if it is possible to draw any inferences as to the general tendencies of the Bantu vertebral column, whether towards increase of the lumbar column at the expense of the sacrum or conversely, or towards an increase of both lumbar and sacral series at the expense of the coccyx.

Instability of the region L. V, S. I is shown clearly in the graph in fig. 1. Apart from abnormalities, such as spina bifida, which may affect any part of the vertebral column, the following have been met:

(1) fusion of the twenty-fourth vertebra to the sacrum, 1 example (Section IV A).

(2) transitional characters in the twenty-fifth vertebra, 3 examples (Section IV A).

(3) partial separation of the twenty-fifth vertebra from the sacrum, 7 examples (Section IV B).

Partial release of the twenty-fifth vertebra from the sacrum is commoner than inclusion of the twenty-fourth in the proportion 10 to 1. Therefore any tendency that may be deduced towards change in the regional composition of the lumbar column is in the direction of increase.

In about a fifth of cases, or 17 out of 87, the sacrum increases to 6 vertebrae, by inclusion of the thirtieth vertebra, whether by process of sacralisation or not.

The tendency on the part of the sacrum to acquisition of the thirtieth vertebra is stronger than the tendency to the release of the twenty-fifth, in the proportion 17 to 7. The inference is that, in the evolutionary sense, acquisition of the thirtieth vertebra precedes, and perhaps makes possible, the release of the twenty-fifth. This inference is supported by the fact that only 2 out of 17 six-piece sacra show separation of the twenty-fifth vertebra. Transitional forms at the lumbo-sacral junction show that the thirtieth vertebra has been incorporated in the sacrum in 2 out of 3 specimens, i.e. in specimens 2 and 3 described in Section IV A.

In the Bantu vertebral column two tendencies seem clear: (1) a tendency of the lumbar column to increase to 6 vertebrae, (2) a tendency of the sacrum to increase to 6 units, which is the stronger of the two. A third inference follows, while there is a recognisable tendency for the lumbar column to increase to 6, a tendency which achieved completion once in my series of 82 columns; and a tendency for the sacrum to increase to 6, which is achieved 17 times in a series of 81 sacra: ultimately both these tendencies can only be effected at the expense of the coccygeal series of vertebrae.

My fourth example of a twenty-fifth vertebra with transitional characters (Section IV A, Specimen 4) exhibits a tendency counter to the general tendencies of the Bantu column in a partial separation of the twenty-fifth vertebra without acquisition of the thirtieth.

The statement of Le Double, which I have borrowed from Benassi (14), shows that in European sacra the four-piece condition is rare. Out of a series of 1528 sacra 170 or 11·1 per cent. were of six-piece, 1341 or 87·7 per cent. were of five-piece, and 17 or 1·2 per cent. of four-piece dimensions. (Le Double.)

In my Bantu series of 81 sacra 17 contained 6 vertebrae, and 64 contained 5; no specimen showing complete reduction to a four-piece sacrum was found. These figures admit a comparison of the stability of the Bantu sacrum with that of the European. If the proportion 64 to 81 for the Bantu be rendered as a percentage, a value of 79 per cent. emerges, which may be compared with 87·7 per cent. for the European, which is the proportion in which the sacrum maintains the human mode of 5 units. A notably higher value for the occurrence of the six-piece condition, 21 per cent. compared with 11·1 per cent., is shown in the Bantu.

VI SPINA BIFIDA

The failure of union in the mid-dorsal line of the two lateral elements from which the neural arch and dorsal spinous process are developed constitutes spina bifida. The condition under consideration corresponds to the "spina bifida occulta" of clinicians and pathologists, i.e. non-union of the halves of the neural arch, but without separation and without protrusion of the spinal membranes.

An example is shown in the lower of the two vertebrae in fig. 7.

It is unfortunate that there should be unconformity between the terminology of the anatomist on the one hand, and that of the pathologist and the clinician on the other.

"Spina bifida" rendered in English should be exactly equivalent to "bifid spine." While the meaning of "spina bifida" has been given above, "bifid spine" in the vocabulary of anatomy would indicate the bipartite condition peculiar to the spinous processes of the cervical vertebrae.

Fig. 7

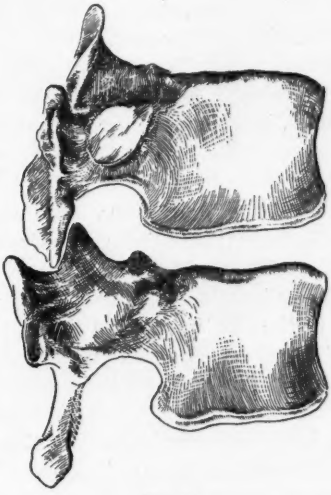

Fig. 8

Fig. 7. This figure shows the eleventh and twelfth thoracic vertebrae of skeleton No. 157 from the dorsal aspect. Both vertebrae are spineless and the lower, twelfth thoracic, exhibits spina bifida in addition.

Fig. 8. This figure shows the eleventh and twelfth thoracic vertebrae of skeleton No. 157 from the right lateral aspect. Absence of spinous processes in both specimens is well shown. The articular area on the twelfth thoracic body for the head of the twelfth rib is indistinct in the drawing but quite evident in the specimen, though somewhat reduced in size. The twelfth thoracic vertebra, on the left, has already been remarked as the subject of spina bifida.

Even if a usage, in itself ambiguous, is permitted by custom to British authors, because uncertainty seldom arises when the context is clear, it is still regrettable that the English "bifid spine" and the Latin "spina bifida" should convey two different meanings. Nor is this a point of mere pedantry; a nicety of terminology in this respect is desirable, because even if the discussion were limited to the cervical vertebrae, a bifid spinous process is almost as much a matter for comment in Bantu skeletons, on account of its rarity, as is spina bifida.

Perhaps, if the word "spina" is to be retained, "spina fissa," or split spine,

would more exactly convey the meaning now attached to "spina bifida." "Bifurcate spine" or "spina bifurcata" would be more appropriate to the condition of the cervical spinous processes of the European.

Occurrence of spina bifida

Twenty-three vertebrae exhibiting spina bifida were found in the examination of 82 skeletons. Expressed as a percentage of the 1936 vertebrae, this gives a value of 1·19 per cent. nearly. The survey by Willis (16) of the collection in the Hamann Museum shows the occurrence of spina bifida in only 9 out of 748, or in 1·2 per cent. of columns. It must be emphasised that the value given above, viz. 1·19 per cent. refers to vertebrae and not to columns; no less than 15 out of 82 Bantu columns exhibited spina bifida. I have stated earlier that the 82 columns reported on in this paper represent a fair sample of the Bantu peoples, in which case the high proportion of spina bifida is striking.

Distribution of spina bifida in the vertebral column

The two graphs in fig. 9 are constructed on the same lines as fig. 1. On the horizontal base line each unit of the vertebral column is represented, and each vertebra with spina bifida is represented in the lower graph above its serial designation by a black square.

In the Bantu, as fig. 9 shows, spina bifida occurs most frequently in the first sacral vertebra, next in point of frequency in the atlas and twelfth thoracic vertebra equally, and to a lesser degree at the upper end of the thoracic column. There is a general similarity between the spina bifida graph in fig. 9 and the graph of the general abnormalities in fig. 1, in that the incidence falls most on the regions where a junction of vertebrae of different types occurs, and least on the middle members of each series.

In the Hamann Museum, according to Willis, the last praesacral vertebra was affected in each of 9 columns. In 7 columns the last praesacral was the twenty-fourth, or true fifth lumbar, and in two columns the twenty-fifth, or a sixth lumbar. Kirmisson (17) finds spina bifida to be most frequent in the cervical and lumbar regions in French children, and states that spina bifida may be found in both regions in the same column. Kirmisson, in explanation of this distribution, states that the normal closure of the medullary groove in the embryo takes place first in the dorsal region, and consequently that failure of union would be expected to be least frequent in that region. This view is scarcely confirmed by the graph in fig. 9. Neither is Willis' finding of the highest incidence on the last praesacral vertebra. In this Bantu series the first sacral, or the twenty-fifth vertebra, rather shows the highest incidence of spina bifida.

The number of spina bifida vertebrae in a single column

Fifteen vertebral columns contained 23 vertebrae the subjects of spina bifida; 11 of these columns exhibited solitary specimens and 4 multiple

specimens. The details of number and distribution in each column are given in Table I.

In order to further point the extraordinary liability of the Bantu vertebral column to spina bifida, it need only be stated that Kirmisson finds spina bifida to be usually single, and Willis found more than one vertebra (and then only two, L. IV and L. V) affected in one only of his 9 cases. The greatest number in any one Bantu column is 4.

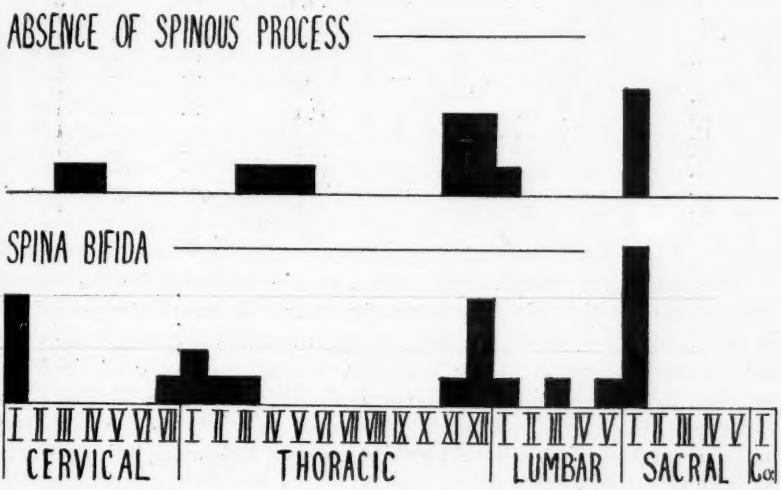
ABSENCE OF SPINOUS PROCESS
SPINA BIFIDA
I II III IV V VI VII I II III IV V VI VII VIII IX X XI XII I II III IV V I II III IV V I
CERVICAL
THORACIC
LUMBAR
SACRAL
Co

Fig. 9. This figure represents in graphic form the distribution of spina bifida and of absence of spinous processes in the vertebral column. The graphs of these two conditions are set out together for comparison. The distribution of the condition of absence of spinous processes is set out in the upper graph and spina bifida in the lower graph. Each abnormal vertebra is represented by a black square. The designation of the vertebrae is set out on the base line; the vertebrae are enumerated from the head tailwards, from left to right along the base line.

Asymmetry of spina bifida

While the division of the vertebral arch and spinous process is usually symmetrical, it is not uncommon to find a larger bony mass on one side or the other. Moreover, this may be the case even though the fissure apparently occupies the mid-line of the body. Asymmetry is present in 6 out of 23 examples of spina bifida in this series.

In the table the 23 specimens of spina bifida are classified as follows: (1) symmetrical, (2) preponderance of bone on the right side, (3) preponderance of bone on the left side. A reference to the table will show that symmetry, right preponderance and left preponderance are found in 17, 5 and 1 specimens respectively. In a majority of specimens right preponderance is present if there is not symmetry. Indeed, of the 11 solitary vertebrae which display spina bifida, symmetry is found in 8 and right preponderance in 3.

Table I. ***Spina Bifida***

		Vertebrae with spina bifida							
		Cervical	Thoracic	Lumbar	Sacral	Symmetry	Right prepond.	Left prepond.	Total
1.	179	I	XII	III, V	—	L. III, C. I	L. V	L. III	4
2.	157	I	XII	I	—	C. I, Th. XII	L. I	—	3
3.	205	—	XI, XII	—	—	Th. XI, XII	—	—	2
4.	235	—	I, II, III	—	—	Th. I, II, III	—	—	3
5.	188	—	XII	—	—	—	Th. XII	—	1
6.	284	—	—	—	I	—	S. I	—	1
7.	286	—	—	—	I	—	S. I	—	1
8.	140	VII	—	—	—	C. VII	—	—	1
9.	216	I	—	—	—	C. I	—	—	1
10.	195A	I	—	—	—	C. I	—	—	1
11.	307	—	—	—	I	S. I	—	—	1
12.	309	—	—	—	I	S. I	—	—	1
13.	236	—	—	—	I	S. I	—	—	1
14.	232	—	I	—	—	Th. I	—	—	1
15.	246	—	—	—	I	S. I	—	—	1
	Totals	5	9	3	6	17	5	1	23

The significance of this finding must remain uncertain for the present. Further investigation might show that right preponderance is the general rule in asymmetrical spina bifida, or that right and left preponderance occur with equal frequency. In the first case, general occurrence of right preponderance in association with the general right-handedness of man would suggest a causal relationship. A physical connection between the upper limb and the vertebral spines is to be found in the muscles trapezius, latissimus dorsi and the rhomboids.

It is unfortunate that the only example of left preponderance in this series should occur in a column in which symmetry, right preponderance and left preponderance are all associated together. Even were it proved that this individual was left-handed, it would not be possible to attach importance to the circumstance. It might be urged that this point of "handedness" should be included in the data attached to skeletons in collections.

Absence of spinous processes in spina bifida

It would not be surprising if vertebrae which show evidence of failure of union of the two halves of the neural arch should also show evidence of maldevelopment of the spinous process, which is derived from the same two elements. This has not proved to be the case, as the spinous processes are usually normally developed in spina bifida. Only 5 out of 23 specimens of spina bifida have shown absence of spinous processes or their reduction to rudimentary proportions.

In column No. 205 the eleventh and twelfth thoracic vertebrae exhibit spina bifida and absence of spinous processes at the same time. A third example is in the twelfth thoracic vertebra of No. 157. Two further examples of both conditions are in the first sacral vertebrae of columns 246 and 307.

Spina bifida of one part of the vertebral column has been found associated with absence of spinous process in another part in 3 columns. In No. 157 C. I, Th. XII and L. I exhibit spina bifida, but Th. XI and XII are spineless. These two vertebrae are seen in dorsal view in fig. 7 and in right lateral view in fig. 8. In column No. 284 absence of spinous processes in Th. II, III and IV was associated with spina bifida of S. I.

VII. ABSENCE OF SPINOUS PROCESSES

The condition of absence of spinous process, or virtual absence on account of reduction to rudimentary proportions, has already received some notice in connection with spina bifida in the preceding section, and has been illustrated in figs. 7 and 8.

Sixteen examples were found in 10 vertebral columns. Of these 5 only were of solitary vertebrae, 11 were multiple examples, being contained in 5 columns. One of the solitary examples was in the eleventh thoracic vertebra (No. 152), but all the others were in the first sacral vertebra.

Fig. 9 has been constructed to show in graphic form the distribution of both spina bifida and absence of spinous process in the vertebral column. A general correspondence in distribution of both conditions, especially in the greatest incidence which is the first sacral vertebra, is to be noted.

In view of the similarity of the regional distribution of spina bifida and of absence of spinous processes, it is remarkable that the association of both conditions in the same vertebra occurred in no more than 5 vertebrae. It may be stated again that this Bantu series contains 23 specimens of spina bifida and 16 of absence of spinous process. Willis holds a strong view of the relation of the two conditions, which my findings hardly confirm, when he states (18) "this defect is, of course, a very imperfect form of spina bifida, and should be so recognised."

Spina bifida and absence of spinous processes in the sacrum

The general similarity of distribution between spina bifida and absence of spinous processes already noted breaks down in the sacral region. The series of skeletons which has provided the material for this paper includes 78 sacra which are perfect in the details of their dorsal arches. These sacra have been examined for spina bifida and for absence of spinous processes. Though spina bifida of the fifth sacral unit is generally accepted as a normal condition in man, it must be remarked, not only is spina bifida frequently absent from the fifth sacral unit, but spina bifida frequently is present in the fourth and occasionally in the third sacral units in the Bantu.

The conditions found in 78 Bantu sacra are as follows:

	I	II	III	IV	V
Absence of spinous processes	4	6	10	4	0
Spina bifida	3	0	1	26	69
Normal spinous process	70	72	67	29	6
Spinous process divided *not* spina bifida	1	0	0	19	3

It seems that the tendencies of spina bifida and of absence of spinous processes, at least in the sacrum, are divergent; where spina bifida is least, in the second and third units, absence of spinous processes is most evident.

The inference is the contrary of that expressed by Willis (vide supra) that absence of spinous processes is "an imperfect form of spina bifida." The view that spina bifida and absence of spinous processes are different, though doubtless related events, is supported by two observations. First, the size of spina bifida spines is usually normal, and secondly, the association of the two conditions in one vertebra is uncommon (see Section VIII).

I prefer the view that absence of spinous processes in a vertebra, whether the subject of spina bifida or not, is determined by some other factors, such as muscular development, attitude and the like during the growth period.

In the lower parts of the sacrum it is not uncommon to find division of the spine without division of the arch. The position of the normal spine is represented by two low tubercles separated by a cleft, of which the floor is formed by the union of the two laminae. In this case the divided spine is always much reduced in size. The distribution of this condition is shown above.

It is evident that more factors than one must be concerned in the production of the following different states:

(*a*) spina bifida with normal sized spine;
(*b*) spina bifida with absence of spine;
(*c*) absence of spine apart from spina bifida;
(*d*) division of a reduced spine without spina bifida.

VIII. ABNORMALITIES OF THE SIXTH AND SEVENTH CERVICAL VERTEBRAE

As the graph in fig. 1 shows, the cervico-thoracic junction in some measure resembles the other inter-regional junctions in being the site of an "outcrop" of abnormalities, but the abnormalities in this place are far fewer than at the lumbo-sacral or at the thoracico-lumbar junction. Besides one seventh cervical vertebra which was the subject of spina bifida, there are four abnormal specimens of the seventh and 1 of the sixth cervical vertebra, in all of which the abnormality lies in the transverse process.

(A) *Cervical rib*

Three examples of short cervical rib were found in two skeletons. In skeleton No. 239 the rib is bilateral and measures 24 mm. on the right and 22 mm. on the left side. On each side the rib is slightly movable and articulates with the body and the "transverse process" by two small facets.

In a second skeleton (No. 281) the rib is present on the right side only. It articulates with the seventh vertebra by two facets as in the other case, but is shorter, measuring 19 mm. This rib is also slightly movable, a quality which is asserted by Humphry [19] to be invariable in a cervical rib.

The incidence of cervical rib in this series is 3 in 82 seventh cervical vertebrae. As the potentialities for development of cervical rib are bilateral, the incidence would be more exactly represented as 3 in 164, or, it might be stated, cervical rib develops in 1·22 per cent. of potential sites in the seventh cervical vertebra.

(B) *Reduction of the transverse process*

In two columns (Nos. 159 and 221) the transverse process is almost rudimentary. In both cases the condition is bilateral, and the specimens are so similar that one description may suffice for both. The transverse processes are very short and project laterally scarcely further than the articular processes. The transverse processes taper rapidly to a pointed tip which is directed downwards and slightly backwards. The anterior surfaces are curved with forward concavities. The grooves for the seventh cervical nerve are found on the upper surfaces of the pedicles, but are not continued on the upper surfaces of the transverse processes, which bear no trace of differentiation into anterior and posterior tubercles. In each case the spinous process is normally developed. In column No. 221 the abnormality described is the only one on the column, but in No. 159 a further abnormality is found in the transverse process of the sixth vertebra, in the absence of the vertebrarterial foramen.

It would be thought that the relative bulk and prominence of the transverse process of the seventh vertebra was as constant a feature of the cervical column as the prominence of the spinous process of the same vertebra. It might perhaps be suggested that costal elements are missing from these two cervical vertebrae. This explanation is improbable, because the vertebrarterial foramina are present in the reduced transverse processes. In No. 159 these foramina are almost as large in the seventh as in the fourth or fifth vertebrae, though in No. 221 they are both very small.

I should expect that reduction of the transverse processes to the exiguous proportions exhibited by these specimens is rare in view of their functional importance. Besides giving attachment to the muscle scalenus posterior, the seventh transverse process gives attachment to Sibson's fascia, which is to be regarded as the essential suspensorium of the pleural apex. I have written elsewhere(20) on the fascial attachments of the seventh transverse process in describing a fibrous band, representative of the muscle scalenus pleuralis, which connects the transverse process to the first rib.

(C) *Absence of the vertebrarterial foramen*

This foramen, usually so characteristic of the cervical vertebrae, is absent from the transverse process on the left side of the sixth vertebra in skeleton No. 159. In no other respect is this vertebra abnormal. The neural groove and the two tubercles of the transverse process are well marked, and the tubercles of "Chaissaignac" on the front of the transverse process are unusually well developed. The seventh vertebra of this column has already been noted on account of reduction of its transverse processes.

IX. MALFORMATION OF THE BODY OF A THORACIC VERTEBRA

A wedge-shaped deformity of the fifth thoracic vertebra was found in the skeleton of a male Basutu, aged 40, No. 262. In the absence of pathological change in the vertebral column or in the skeleton generally, this deformity must be considered a developmental phenomenon. A lateral view of the fourth, fifth, and sixth thoracic vertebrae is shown in fig. 10.

When the thoracic vertebrae were assembled and viewed from the dorsal aspect, the spines, transverse processes and articular processes seemed to form

an uninterrupted and uniform series; the general reduction in size and the deformity of the fifth member were revealed in a lateral view.

The fifth vertebra is not only wedge shaped, but shallower than its neighbours in the vertical measurements of the anterior and posterior surfaces of the body. While the anterior measurements for the fourth, fifth and sixth thoracic vertebrae are, respectively, 16, 10 and 17 mm., the posterior measurements are 16·5, 13 and 19 mm. The wedge-shaped character is shown by the proportions that the anterior depths bear to the posterior depths of the vertebral bodies; for the fourth this proportion is 1·03, for the sixth 1·12, and for the abnormal fifth vertebra 1·3. The intervals between the centres of the articular facets for the heads of the ribs, measured across the bodies of the vertebrae, correspond exactly with the measurements for the posterior depths

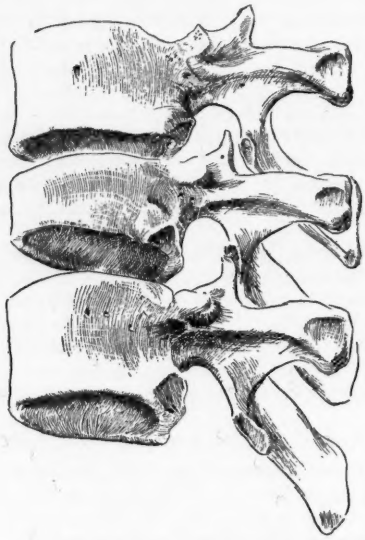

Fig. 10. This figure represents the left lateral and slightly inferior view of the fourth, fifth and sixth thoracic vertebrae of skeleton No. 262. The spinous, transverse and articular processes present no abnormality. The body of the fifth vertebra is wedge shaped, with the narrow end anterior.

given above. The separation between the fifth and sixth ribs must have been less than that between the fourth and fifth, or that between the sixth and seventh ribs. The ribs, it is inferred, must have been crowded, as they do not seem to have been distorted. It also seems probable that some kyphosis must have been present, though there is no record of a deformity noted during life.

The frequency of occurrence of a wedge-shaped deformity of the vertebral body in this Bantu series is 1 in 1936, or ·057 per cent. of vertebrae.

X. ABNORMALITY OF THE LUMBAR TRANSVERSE PROCESSES

The abnormality to be described in this section is one to which I can find no reference whatever in the literature available.

The third and fourth lumbar vertebrae both exhibit, on the same side, a bifurcate condition of their transverse processes. While the usual transverse processes are present, and normal except for a slight elongation, each vertebra bears a second projection which arises from the base of the transverse process and lies in a more anterior plane. These second projections from the third and fourth lumbar vertebrae are directed towards each other and effect a contact but not a fusion with each other.

In order to obtain a photograph, the two vertebrae were articulated together in a natural position with plasticene occupying the place of the intervertebral disc. In fig. 11 both anterior and posterior views of the third and fourth lumbar vertebrae are shown.

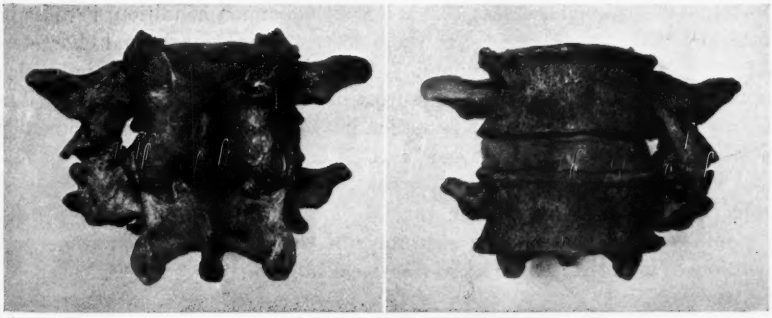

Fig. 11. On the left is shown a dorsal view, and on the right a ventral view of the third and fourth lumbar vertebrae of skeleton No. 332. It can be clearly seen in both photographs that a downward projection from the lateral process of the third vertebra meets an upward projection from the lateral process of the fourth. The photograph on the right shows that these two processes lie in a plane anterior to the transverse processes. Both projections are actually based on the pedicles and the roots of the transverse processes.

The bony projection from the third lumbar vertebra is approximately cylindrical in form, has its origin from the pedicle and the root of the transverse process and is directed forwards and downwards to the left. This projection measures 1·3 cm. in length on its posterior and 2·3 cm. on its anterior surface, while the greatest thickness is 2·2 cm. The transverse process of the third lumbar vertebra on the right side is 3·5 cm. and on the left side 4·4 cm. in length.

The projection from the fourth lumbar vertebra is also cylindrical, but shorter than the other and somewhat thicker. This projection is directed upwards, forwards and slightly to the left, and is based on the pedicle and on the root of the transverse process. The projection from the fourth lumbar vertebra measures 1·2 cm. along the anterior surface and ·8 cm. along the

posterior surface, and 2·4 cm. in its greatest thickness. The right transverse process is 2·7 cm. in length and the left 3·3 cm.

Possibly the two bony outgrowths represent some abnormal development of the costal elements of the lumbar transverse processes.

XI. ABNORMALITY OF THE TWELFTH THORACIC VERTEBRA

In the twelfth thoracic vertebra of skeleton No. 307 characters intermediate between those of a lumbar and those of a thoracic vertebra were noted. This same column was the subject also of congenital abnormalities, to be noted in the next section (Case IV), which affected the fourth and fifth lumbar vertebrae.

On the right side of the body of this vertebra is the normal articular facet for the head of the twelfth rib, while on the left side there is no trace of an articulation and the twelfth rib is lacking. This vertebra, therefore, is thoracic on the right side and lumbar on the left.

While it is recognised that this is a not uncommon condition, it must be remarked that, out of 81 twelfth thoracic vertebrae, transitional characters appear in this position in one only. In the same series, vertebrae indicating more or less transition of characters from one region to the next appeared as follows— at the cervico-thoracic junction in two, at the lumbo-sacral junction in four and at the sacro-coccygeal junction in seventeen columns.

I have no statistics available for comparison, but I should have expected from my experience in London that a "lumbarisation" of the nineteenth vertebra was commoner than any other of the transitional conditions just mentioned, save that at the sacro-coccygeal junction.

XII. CONGENITAL DIVISION OF THE VERTEBRAL LAMINA

A type of abnormality of particular interest to the orthopaedist and obstetrician, no less than to the anatomist, is to be found in congenital division of the vertebral lamina.

The particular interest of this abnormality lies in the fact that congenital division of the lamina may be antecedent to forward dislocation of the body of the fifth lumbar vertebra from the upper surface of the sacrum, i.e. to the condition known as spondylolisthesis. The consequences of dislocation may include not only deformity of the vertebral column, but actual obstruction to the brim of the pelvis.

Spondylolisthesis did indeed occur in the series of skeletons under review, and obstruction to the pelvic brim caused the death of the patient from rupture of the uterus during parturition.

When the first example of the condition was found in these Bantu skeletons, I was, for a time, in some doubt if a congenital abnormality or the effect of an unusual fracture had been discovered. Having resolved this doubt in favour of a congenital abnormality, I wish to indicate clearly the site of division in

the vertebra by the use of the term "congenital division of the lamina." The lamina is divided transversely between the superior and the inferior articular processes in 6 vertebrae which are contained in 5 columns. Examples of the lesion are illustrated in figs. 12 and 13, and are described below.

Case I. (No. 159.) The abnormal vertebra is the fourth lumbar of a male Xosa, aged 45, and is shown in fig. 12 from the inferior aspect. The right lamina only is divided rather nearer to the superior than to the inferior articular process. In a corresponding position on the left lamina there is a rough line on the surface of the bone, which is somewhat indistinct in the drawing, though more easily traced on the inferior surface.

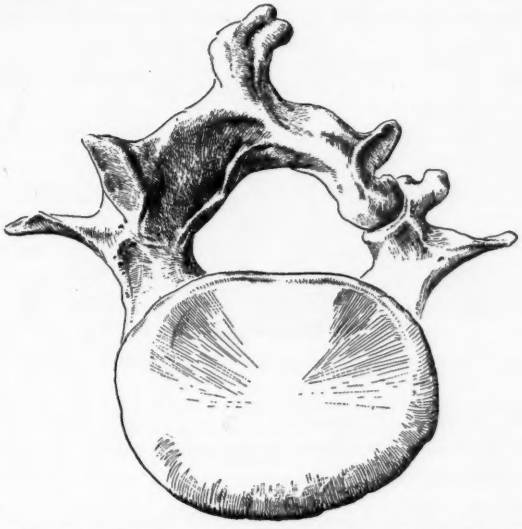

Fig. 12. This figure shows the appearance of the fourth lumbar vertebra of skeleton No. 159 from below. The division of the right lamina between the superior and the inferior articular processes is represented on the right side. The greater thickness of the left pedicle and lamina, and the lateral projection of the left side of the arch are shown.

Asymmetry is very obvious in this bone. The left lamina is much thicker and is longer than the right, with the result that the inferior articular process on the left side projects laterally further than the superior articular process, and further even than the mammillary process of the same side. It can be seen in fig. 12 that the left lamina is reinforced by a bar of bone that extends from the pedicle to the middle of the dorsal arch. The left pedicle is stouter than the right and the body is more bulky on the same side. The spine shares in the asymmetry, being slightly deflected to the left. Except for the seventh cervical vertebra (*q.v.* Section VIII), this column presents no other abnormality, and there is no evidence of deformity during life.

Case II. (No. 280.) Fig. 13 shows in dorsal view the fifth lumbar vertebra of a male Shangaan, aged 36. In the dorsal view, a cleft on each side traverses the lamina immediately distal to the superior articular facets. The effect is to divide the vertebra into two quite separate parts: (1) the dorsal arch with the spine and the inferior articular processes, and (2) the body with the two pedicles and the superior articular processes.

The cleft, though bilateral, is not quite symmetrical in its effect. The dorsal arch is thicker and stronger on the left side, and the spine is deflected to the left. The left pedicle is slightly the thicker and the vertebral body bulks more on the left than on the right side. There is no abnormality in the column except sacralisation of the thirtieth vertebra, and no sign of deformity.

Case III. (No. 303.) The fifth lumbar vertebra of a male Griqua, aged 57, furnishes a third specimen. A bilateral cleft, situated just distal to the superior articular processes, separates that part of the dorsal arch which bears both the spine and the inferior articular processes from the rest of the vertebra. There is no abnormality of the vertebral column except sacralisation of the thirtieth vertebra.

Case IV. (No. 307.) In this skeleton, that of a male Shangaan, aged 60, two lumbar vertebrae, the fourth and fifth, both exhibit division of the laminae between the superior and the inferior articular processes. The twelfth thoracic vertebra is abnormal, but there is no general abnormality of the column.

Case V. (Fig. 248.) This specimen, presenting the condition of spondylolisthesis, was found in the skeleton of a Bechuana woman, aged 42.

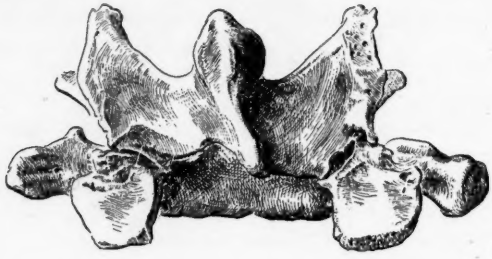

Fig. 13. This figure represents the appearance of the fifth lumbar vertebra of skeleton No. 280 from the dorsal aspect. Separation of the dorsal arch brought about by bilateral division of the laminae can be seen. The clefts in the laminae are immediately distal to the superior articular surfaces.

I have described this specimen, together with the other examples of congenital division of the lamina, in the *British Journal of Surgery* (vol. XVI, no. 63, 1929). I do not propose, therefore, to do more than remark that in the skeleton the following facts are clear: (1) the inferior articular processes of the fifth lumbar vertebra, with the dorsal arch and spine, have adhered to the articular processes and the dorsal arch of the sacrum; (2) the body of the fifth lumbar vertebra, bearing the rest of the vertebral column above it, had during life become separated from the dorsal arch of the fifth lumbar vertebra, and is lying in front of the first sacral vertebra, supported by a shelf of thin bone of new formation.

For a full description of the specimen of spondylolisthesis, and a full discussion of the circumstances that favour the explanation of congenital abnormality, the reader is referred to my earlier article.

Discussion.

It is easy to understand that when the inclination of the lumbar column on the sacrum approaches a right angle, the influence restraining the fifth lumbar vertebra from forward displacement is to be found in the locking of the inferior articular processes of that vertebra in the superior articulation of

the sacrum. Indirect violence applied through the long axis of the trunk, as in jumping or stumbling when carrying a weight on the back, might effect the separation of the dorsal arch together with the inferior articular processes. Sir Arthur Keith (21) considers that this effect might come about as a result of indirect violence, and independently of congenital weakness in the attachment of the dorsal arch. He states, "I know of no evidence which leads me to suppose that the separation of the arch of the last lumbar vertebra is the result of maldevelopment."

In this connection the following considerations are important:

(1) In Case I is recorded unilateral division of the lamina which is difficult to explain by the supposition of injury; moreover this case is in the fourth lumbar vertebra. There is never, normally, an angle between the fourth and fifth lumbar vertebrae comparable to that between the fourth and fifth vertebrae, so Keith's explanation would scarcely satisfy in this case.

(2) In Case IV both the fourth and fifth lumbar vertebrae are affected. Injury would scarcely account for the separation of two dorsal arches, and, in view of the difference of angulation referred to above, the same injury could not explain both.

(3) In Case III the lumbo-sacral junction does not display angulation more than normal; indeed, the contrary is the truth; the lumbar and the sacral series of vertebrae are more nearly in a straight line than they are in the majority of columns.

(4) Reconstructions of the vertebral columns do not display deformity except in Case V.

Prof. Peter Thompson (22), who contributes the Section on Osteology to *Morris' Treatise on Anatomy*, writes as follows: "the fifth lumbar exhibits in some cases a special mode of ossification in the arch. Instead of two centres there are four—one on each side for the root, transverse process and superior articular process, and another on each side for the lamina, inferior articular process and the lateral half of the spinous process."

It is recorded, therefore, that the dorsal arch of the lower lumbar vertebrae may ossify in two parts, which, by Prof. Thompson's account, correspond to the two parts found in my specimens.

It seems most probable that the condition described as congenital division of the lamina is the outcome of a lack of fusion between the two skeletal elements from which, in the lower lumbar vertebrae, the dorsal arch may be developed.

The survey of 748 vertebral columns in the Hamann Museum by Willis (23) revealed a like condition in 31, i.e. in 4·28 per cent. of columns. Unilateral division of the lamina was found (always on the right) in 8, bilateral division in 23 vertebrae. Association with spina bifida was noted in 5 vertebrae, and spondylolisthesis is also described.

In Willis' series congenital division of the lamina occurred in the third lumbar vertebra in 2 columns, and in the last praesacral vertebra in 29 columns.

The last praesacral vertebra was the twenty-fourth, i.e. the normal fifth lumbar, in 26 columns, and was the twenty-fifth, or sixth lumbar, in 3 columns.

Willis quotes Le Double(4) who, in describing 11 such cases of his own observation, contributes a summary of 33 such cases recorded in the literature. Apparently, congenital division of the vertebral lamina has been recorded in the first sacral and the first lumbar vertebrae on 1 occasion each, in the fourth lumbar twice and in the fifth lumbar on 29 occasions.

The greatest incidence of congenital division of the lamina is shown both by Willis and Le Double to be on the fifth lumbar, which is normally the last praesacral vertebra. In the Bantu there seems some tendency for this defect to shift from the last praesacral position, which in Willis' and Le Double's combined series was the site of congenital division of the lamina in 58 out of 64 vertebrae.

In the Bantu, the last praesacral vertebra was the subject in three columns (Cases II, III, V), the penultimate praesacral vertebra once (Case I), and the last two praesacral once (Case IV). In the Bantu, moreover, the proportional incidence is high, viz. 5 columns out of 82. If it be permitted to state this proportion as a percentage, a value of about 6 per cent. of columns results, which may be compared with Willis' finding of about 4·28 per cent. for a mixed American White and Negro material.

XIII. NUMERICAL VARIATIONS

The vertebral column of man contains 24 vertebrae on the cephalic side of the sacrum. The sacrum contains 5 vertebrae, and the coccyx a number which varies from 1 to 3 or 4. These proportions are expressed by the formula C. VII, Th. XII, L. V, S. V, Co.?, a formula which, on the whole, is so constant and so widely accepted as a normal that for the purposes of this paper it will be regarded as a standard.

Variation of this formula has been found in 7 of the vertebral columns under review.

Examples of numerical variation

(1) Increase of the lumbar vertebrae to 6, without alteration of the other series, was found in the skeleton of a male Zulu (No. 190). The praesacral vertebrae number 25, and the sacrum is normal, so the vertebral formula for this column is C. VII, Th. XII, L. VI, S. V.

(2), (3), (4). In Section IV A are described three specimens of abnormal sacra, in which the twenty-fifth vertebrae exhibit characters which are transitional between lumbar and sacral. The formulae which apply to the praesacral vertebrae in these three columns are alike, although there are considerable differences in the structural details of the sacra.

Specimen 2, Section IV A, is that of a sacrum whose first piece is largely separated from the sacrum, and contributes a very reduced share to the formation of the sacro-iliac-joint.

Specimen 3, Section IV A, is that of a sacrum whose first piece presents lumbar characters on the one side, and sacral features on the other. In both these columns a vertebra of transitional type intervenes between the lumbar and the sacral series, and this formula emerges C. VII, Th. XII, L. V + X + S. V.

A second example of the twenty-fifth vertebra presenting lumbar form on one side and sacral on the other is found in column 282, Section IV A 4. The whole sacrum, however, differs from the last in that the sacral vertebrae following on the abnormal twenty-fifth are reduced in number. The praesacral vertebrae number 24, and the formula is C. VII, Th. XII, L. V + X + S. IV.

Relative regional variation

In certain columns variation in the number of vertebrae of one designation is compensated by variation in the opposite direction in the adjoining region, leaving the total unaltered. This phenomenon was noted in three columns.

(1) In column No. 199 an increase in the number of lumbar vertebrae is associated with a reduction in the number of thoracic vertebrae. The praesacral vertebrae number 24, and the vertebral formula is C. VII, Th. XI, L. VI, S. V.

(2) In column No. 203 a similar condition obtains in the thoracic and lumbar series and, in addition, a six-piece sacrum is present. The vertebral formula is C. VII, Th. XI, L. VI, S. VI, Co.?, and the praesacral vertebrae number 24.

(3) A vertebra of transitional character is interposed between the thoracic and lumbar series in column No. 307, and is described in Section XI. The praesacral vertebrae number 24, and the formula is C. VII, Th. XI + X + L. V, S. V.

Comment on numerical variation

It has been sufficiently demonstrated that the vertebral column of the Bantu presents a high degree of variability. Apart from numerous examples which exhibit structural abnormality in single components, the numerical content of the Bantu column is not a fixed quantity. We have met examples of columns in which the number of free vertebrae above the sacrum is 25, as well as those in which a vertebra intervenes between the sacrum and the lumbar column and presents transitional or indeterminate characters.

The question naturally arises if there is any discernible principle or law of change in the human skeleton, capable of definition, which underlies these abnormalities or governs their appearance.

Wingate Todd and his colleague Willis, of the Western Reserve University, Ohio, in certain essays on the content of the vertebral column, both in animal types and in a very large collection of human skeletons lodged in the Hamann Museum, have formulated certain principles for the interpretation of many of the aberrations, both in form and in number, exhibited by the vertebral column of man. In addition to the formulation of principles, these authors have furnished figures for the variability of the human columns under their observation which admit of a direct comparison between the vertebral column of the American White and the American Negro on the one hand, and of the Bantu on the other. Wingate Todd (1), in a survey of the vertebral columns of Mammalia, comments on the constancy of seven cervical vertebrae throughout the mammalian series. Though variation of the content of the cervical column is probably the rarest of numerical variations in the vertebral column of man, the content of the thoracico-lumbar series through the Mammalia is very variable. In the same essay the author shows reason for believing that the primitive number of thoracico-lumbar vertebrae in Mammalia is 19, and that

the primitive total number of praesacral vertebrae is 26 (i.e. 19 plus 7). While there is a tendency towards increase of this number in many orders of Mammalia, in Primates and in Man the tendency is towards reduction. Progressive reduction of the thoracico-lumbar column is shown in the anthropoids and in man; the "modal" number of the orang is 16, of the gibbon 18, while the gorilla, the chimpanzee and man have a "modal" number of 17 thoracico-lumbar vertebrae.

Man is, however, characterised by a stability of the "modal" number of 17 thoracico-lumbar vertebrae, which is far higher than that of the anthropoid apes.

Willis (2) has shown that the varying numerical content of different vertebral columns of man may be interpreted in the following way. The majority of columns present the "modal" or average number of 17 thoracico-lumbar vertebrae; a proportion exhibit a tendency to retrace the path of evolution in reversion to a pre-human condition of 18, a tendency which may be effected completely or incompletely; a proportion also exhibit a tendency, with effect complete or incomplete, towards "progression," or further reduction from 17 to 16 of the thoracico-lumbar vertebrae, following the path trodden by the orang, which in this respect is more specialised than man.

Vertebral columns may, therefore, be classified under five heads, according to their content of thoracico-lumbar vertebrae: (1) "18," being complete reversion from 17, (2) "17 plus," incomplete reversion from 17 to 18, (3) "17," the "modal" number of man, (4) "17 minus," incomplete progression or reduction from 17 to 16, (5) "16," being complete reduction from 17.

While the meanings of Groups 1, 3 and 5 are sufficiently obvious, it may be best to give examples to illustrate the meanings of Groups 2 and 4, "17 plus" and "17 minus."

In the category "17 plus" numerous examples have occurred. Earlier in this section reference was made to those skeletons in each of which the first piece of the sacrum, or the twenty-fifth vertebra, exhibits transitional characters. This condition is interpreted as an incomplete reversion on the part of the column to the condition of 18 thoracico-lumbar vertebrae. In two of these cases the twenty-fifth vertebra is obviously of intermediate type, with one half lumbar and the other half sacral. Had this vertebra been completely lumbarised or completely sacralised, the column would have been included in the Group 1 in the one case, or in the Group 3 in the other. The intermediate characters place the column in the Group 2. Partial separation of the first sacral vertebra from the sacrum, in Willis' opinion, constitutes evidence of incomplete reversion on the part of the column to the pre-human mode of 18 thoracico-lumbar vertebrae. I have, therefore, in order to achieve uniformity with Willis, included in this same category of "17 plus" those columns of which the sacra exhibit partial separation of the first vertebra.

In the category "17 minus" I have only one example to record. In Section IV A, Specimen 1, an incomplete stage in "progression" from 17 to

16 thoracico-lumbar vertebrae is recorded. The twenty-fourth vertebra is joined to the sacrum, but retains a number of lumbar characters.

From Willis' report (24) I have extracted figures relating to the American White and the American Negro races which show the proportions of vertebral columns which fall into each of the categories defined above. These figures and corresponding figures for the Bantu are set out in Table II.

Table II

Group Thoracico-lumbar vertebrae	American White (Willis)		American Negro (Willis)		Bantu	
	Number	%	Number	%	Number	%
1. "18": complete reversion	24	3·8	9	4·12	1	1·22
2. "17 plus": incomplete reversion	12	1·9	6	2·75	10	12·19
3. "17"	565	89·4	187	85·78	70	85·36
4. "17 minus": incomplete progression	25	3·95	13	5·9	1	1·22
5. "16": complete progression	6	·95	3	1·38	0	0·0
Totals	632	—	218	—	82	—

Two conclusions may be drawn from Table II:

(1) The stability of the modal number of 17 thoracico-lumbar vertebrae in the Bantu is very similar to that of the American Negro, but distinctly less than that of the American White.

(2) A very striking difference between the American Negro and the Bantu is seen in the proportions of the variants from the modal number. Whereas, in the first, the variations on the one side of the modal number approximately balance the variations on the other side, in the Bantu a definite bias is exhibited on the part of the variants, a bias towards reversion from 17 to 18 thoracico-lumbar vertebrae.

Whether or not examination of a series of Bantu skeletons, comparable in number to the collection in the Hamann Museum, will confirm these findings must be left to the future to decide. The material at present available seems to allow of no other conclusion, if I have understood Willis' argument correctly.

The bias on the part of the Bantu vertebral column, indicated by the figures in Table II, if not created, is at least greatly accentuated by the inclusion in the Group 2 of seven columns whose sacra show partial separation of the first vertebra. It might be objected that undue emphasis has been placed on the significance of this phenomenon. If these seven columns are included in the group of 17 thoracico-lumbar vertebrae, the following figures emerge for the different groups—"17 minus," 1 or 1·22 per cent.; "17," 77 or 93·9 per cent.; "17 plus," 3 or 3·66 per cent.; "18," 1 or 1·22 per cent. In addition to the fact that the bias towards 18 thoracico-lumbar vertebrae is still present, a difficulty which would need explanation is the raising of the stability of the modal number to 93·9 per cent., a figure which is higher than is found in the American Negro or even in the American White. A student of the Bantu skeleton who at every turn has observed instability and an incidence of each

abnormality higher than is recorded in the other races, would admit a high stability of the Bantu skeleton in any respect with scepticism.

Sir Arthur Keith (25) supports Wingate Todd in his main conclusions regarding the shortening of the thoracico-lumbar column in anthropoids from the primitive mode of Mammalia. This Keith considers to be the result of the erect attitude, and he suggests that a secondary lengthening took place in the lumbar column on the assumption of a plantigrade posture. Keith finds the same general tendencies in the human vertebral column as are shown in the analysis of my Bantu material. He states—"In a series of one hundred human skeletons it will be found that some three or four will show a headward sacralisation, while 6 or 8 will show a tailward movement. The evolution of the plantigrade posture has necessitated a lengthening of the loins in man—the tendency of sacralisation in him seems to be in a tailward direction."

The stability of the five-piece condition of the sacrum in the Bantu has been reviewed in Section V. A very strong tendency on the part of the Bantu for the incorporation of the thirtieth vertebra in the sacrum has been noted. If the considerations raised in the preceding paragraphs be held to indicate a tendency for the increase of the thoracico-lumbar column, which implies a tailward shift of the point of attachment of the lower limb, then it must be added that the tendency of the Bantu sacrum supports that opinion. If the mode of fixation of the lower limb girdle to the vertebral column is to remain of the same mechanical order, in spite of a tailward shift of the lower limb, the inclusion of an additional vertebral unit in the sacrum is an obvious necessity.

XIV. SUMMARY AND CONCLUSIONS

In the examination of 82 Bantu vertebral columns a very remarkable abundance of abnormalities has been found.

The survey carried out by Willis on the human skeletons in the Hamann Museum has been utilised for comparing the American White and Negro on the one hand and the Bantu race on the other.

Variations at the lumbo-sacral junction appear to be less common than in the Australian aboriginal, and more common than in the European. The addition of the thirtieth vertebra to the sacrum, whether with sacralisation or without, occurred in 17 columns, indicating a stronger tendency for increase of the sacrum in the Bantu than in the European.

Spina bifida affected 15 out of 82 columns and 1·19 per cent. of vertebrae. In Willis' series only 1·2 per cent. of columns were the subject of spina bifida. Sixteen examples of absence of spinous processes occurred and 23 examples of spina bifida, but only 5 vertebrae showed both conditions. The two conditions are classed together in Willis' survey.

Congenital division of the lamina occurred with remarkable frequency. Five columns out of 82 provided 6 specimens, a proportion which is high compared with Willis' estimate of 4·28 per cent. of columns.

Other abnormalities, such as cervical rib, and abnormalities of the vertebral body and the lumbar transverse processes have been met.

Abnormalities at the lumbo-sacral junction have been interpreted after Willis' method, in terms of the tendency exhibited by the column either to revert to a pre-human condition of 18 thoracico-lumbar vertebrae, or to shorten the column to a condition of 16 thoracico-lumbar vertebrae. The stability of the "modal" number of 17 thoracico-lumbar vertebrae in man is reviewed in the Bantu, and it appears to be practically the same as in the American Negro, but less than in the American White. In the Bantu a tendency is shown towards reversion from 17 to 18 thoracico-lumbar vertebrae, much stronger than the tendency to progression from 17 to 16. In the American Negro these two tendencies are fairly evenly balanced.

The high degree of variability shown in the Bantu may by some be attributed to chance in a small number of skeletons. This may be the case, but such an explanation would be more convincing if the number of abnormalities were made up of any one type of abnormality in an undue proportion. On the contrary, spina bifida, absence of spinous processes, congenital division of the lamina, and variations at the lumbo-sacral junction are all high, and sometimes very high, in their proportional incidence.

It is evident that the Bantu vertebral column is extremely plastic and prone to malformation.

Additional material will show if this present study is of an entirely representative character. I have every expectation that it will prove to be so, because the material is unselected, and, during the period in which I have personally supervised the collection of Bantu skeletons, I have not observed any perceptible falling off in the proportion of abnormalities.

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AXILLARY MAMMA IN A MAN

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THE occurrence of mammary glands in the axilla is a normal condition in certain Mammals (7), such as bats (*Brachyphylla cavernarum*); lemurs (*Galeopithecus volans*), and *Tarsius spectrum*. Although very rare, axillary nipples or mammae may also occur in the human subject. The majority of these cases appear to have occurred in women. Some of the reported cases appear to be not true mammary glands or nipples, but merely hypertrophied sweat or sebaceous glands. This is the case more especially in accessory glands which are atypical in position, namely not in either of the two axillo-inguinal lines. True mammae which have secreted milk have, however, very occasionally been developed in situations other than the axillo-inguinal lines, e.g. on the outer side of the thigh (4). The true axillary mammae are usually symmetrical, and have been developed either on the anterior wall of the axilla, or actually in the fossa. They may be associated with other accessory mammae either above or below the normal pair. In one case reported by Neugebauer (5), a woman had ten mammae, there were three pairs of nipples above the normal, the highest pair lying in the axillae, and there were two accessory nipples below the normal pair. These, however, although they were situated in the mammary lines were not on the same level, the left being considerably lower than the right.

The case, fig. 1, which forms the subject of this paper, occurred in a man, who died aged 67, from "cardiac" and "renal disease." He was excessively fat. The accessory organ, *A*, was situated high up in the hollow of the left armpit. There were no other accessory nipples. The nipple was conical, of large size, 2·3 cm. in height and deeply pigmented. It was situated on the summit of a rounded mass of fat, which gave the appearance of there being a well-developed breast. The subcutaneous veins over this area were congested, and there was a small sebaceous cyst at the base of the nipple.

Microscopical examination showed that the bulk of the swelling was fatty tissue somewhat altered in character by inflammation. The nipple and adjoining tissue at its base was divided for microscopical examination into two parts by a vertical incision passing from base to apex. One half was sectioned longitudinally, the other transversely. At the base of the nipple on one side there were two or three lobules composed of definite acini, lined by cubical epithelium, and near these was a group of tubules lined by a single layer of low columnar epithelium. The other half of the nipple which was cut transversely showed cross-sections of lactiferous ducts, lined by flattened

epithelium, and also what appeared to be unstriped muscular tissue lying in the connective tissue around them. Numerous pigment granules were present in the deeper cells of the epidermis.

The pectoral pair of nipples and areolae, *B*, were in the normal position and had the usual rudimentary appearance of the male mammae. The external genitals had the appearance of the normal male organs, and the secondary sexual characters were typically male, more especially as regards the general conformation of the body, and the distribution of the pubic and facial hair.

The testicles were large, and heavy. Their unusual size was partly due to the very large size of the man, who must have weighed well over 18 stone. They were normal in shape, and there were slight adhesions of the visceral

Fig. 1. Axillary mamma in a man.

and parietal layers of the tunica vaginalis. Both testicles were uniformly firm in consistence. On microscopical examination it was seen that there was a great increase in the amount of fibrous intertubular tissue. In some parts this contained areas which were infiltrated with small round cells resembling lymphocytes. Elsewhere it consisted of a loose areolar tissue containing bundles of white fibres and scattered cells of the lamellar type; these had flattened ovoid nuclei, which were only feebly stained with haematoxylin. There were also a few plasma cells, and a few large polygonal or spheroidal cells, which might be regarded as "interstitial" or "puberty cells" of Leydig. These were, however, very scanty, and did not form the definite groups which are seen in the normal testicle of a man in his prime. The semeniferous tubules

varied in appearance in different parts of the organ. Instead of being uniformly distributed, they were grouped together in bundles surrounded by fibrous tissue. The epithelium in many of the tubules was separated from the basement membrane, and had undergone degenerative changes, so that the cell outlines were indistinct. This was no doubt partly due to "post-mortem" changes, but as some of the semeniferous tubules, and the tubules of the epididymis were fairly normal in appearance, the main cause of the changes was obviously ante-mortem in nature and due to a chronic orchitis. The lumina of some of the semeniferous tubules were filled with a coagulated secretion, containing large multinuclear masses of granular protoplasm, fig. 2. These appeared to be formed by the breaking down and fusion of the epithelial cells. Both the

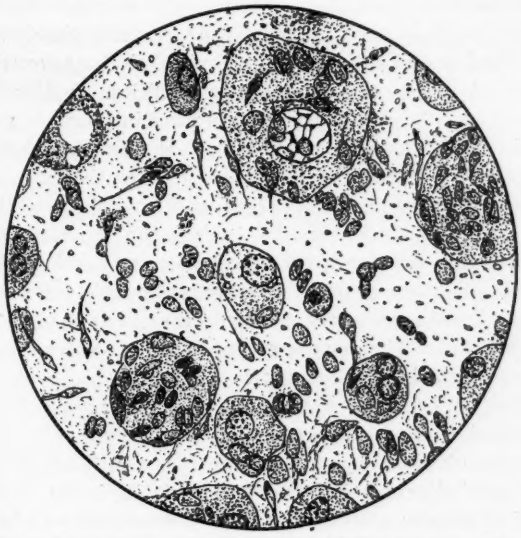

Fig. 2. Spermatozoa and degenerated epithelium in a semeniferous tubule of one of the testes.

coagulum and the multinuclear syncytial masses contained spermatozoa, fig. 2. Owing to post-mortem changes, and degeneration due to chronic inflammation, it was difficult to recognise outlines of cells or to distinguish the supporting cells of Sertoli from the different types of germinal epithelium. Active spermatogenesis, however, must have been in progress shortly before death, as most of the tubules of the epididymis were filled with a coagulated secretion, containing large quantities of spermatozoa.

Many of the rete tubules of the mediastinum testis were dilated, some forming cysts which were visible to the naked eye. They were lined by a continuous single layer of cubical cells. In some places these cells were shed, so as to form masses of detached cells in the lumen of a dilated tubule. The majority of the rete tubules, however, appeared empty, and thus differed

markedly from the semeniferous tubules and tubules of the epididymis, which were filled with secretion containing spermatozoa.

From the standpoint of the present paper, perhaps the most important of the structural changes which have been described above, is the sparseness of the interstitial cells of Leydig. Stress must not be laid on this circumstance, however, since with the exception of the axillary mamma, the secondary sexual characters of the male were pronounced. It is possible, however, that the extreme fatness of the individual may have been partly due to the scarcity of these cells.

The normal growth and activity of the mammary glands have been specially studied in this country by Miss Lane-Claypon and Starling, in the rabbit, and it has been shown by these and other workers that the stimulus which produces the slight enlargement of the mammary glands which attends the pre-oestral and oestral periods in many animals is due to ovarian influence, and more particularly to cells of the ovarian follicles. Further the increased growth of the mammary glands which takes place in pregnancy is believed to be due to a chemical substance, circulating in the blood, which originates in the cells of the corpus luteum. It has moreover been shown by experimental division of the uterine and ovarian nerves, and by division of the lower part of the spinal cord, that the increased growth of the mammary glands during pregnancy is independent of any reflex mechanism acting through the nervous system on the mammary glands. In support of this conclusion, may be recalled the well-known case of pregnancy occurring in one of two pygopagous twins (Rosa-Josepha). "The mammary glands of both twins became similarly and simultaneously enlarged, namely in Rosa who had conceived, and in Josepha who had not become pregnant. Moreover Rosa gave birth to a healthy boy, who was suckled by Josepha as well as by his mother Rosa (8)."

The enlargement which sometimes takes place in the male at puberty is possibly due to a similar chemical excitant circulating in the blood and arising from the genital glands; and the question at once arises as to whether the cells which secrete this substance are the interstitial cells of Leydig (puberty glands) or is there any co-existence of ovarian tissue, with testicular tissue in either of the testes. Further, is the development of female characteristics in these individuals due to a weakening or loss of a dominating or inhibiting influence exerted by the male gonads over the recessive female elements? In the case which I have described there is no indication of ovarian tissue in the genital glands; on the other hand a morbid condition exists, which has caused a degeneration of both semeniferous tubules and interstitial cells. This condition may have been associated with the excessive deposit of fat, but the development of the accessory mammary gland and nipple in this case was most probably a congenital anomaly, and obviously preceded the degenerative changes in the testes.

The chief interest of these cases, and of the normal occurrence of a rudimentary pair of mammary organs in the male, lies in the question as to the

light they may throw on certain aspects of heredity. With regard to the occasional appearance of accessory nipples in the axillo-inguinal lines, Charles Darwin writing in *The Descent of Man*, 1877, makes the following statement, "On the whole we may well doubt whether additional mammae would have been developed in both sexes of mankind, had not his early progenitors been provided with more than a single pair."

Both Darwin and Haeckel were of opinion that the mammary glands were originally developed in the higher Vertebrates as organs acquired for the definite purpose of nourishing the young, and that their continuance and their appearance in both sexes was an example of inheritance of acquired characters. They believed also that the well-differentiated organs with raised nipples of the higher types have been gradually evolved from the normal sudoriferous glands of the skin. This view is held at the present day by most comparative anatomists, and has not been disproved by any of the modern students of heredity. The appearance of the normal pair of nipples in the male is usually regarded as an inheritance of these organs from the female, the maternal influence being manifested in the same way as in the normal development of the Müllerian ducts in the male embryo, and the retention of these in a rudimentary form in the adult. Like the Müllerian ducts, the mammary organs in the male usually remain undeveloped but in exceptional circumstances they make take on an active growth at puberty, and appear in the adult as large pendulous organs, with protuberant nipples, and well-developed areolae. In some instances they have become functional. The stimulus which produces this development in the male is probably a hormone similar to that present in the female circulating in the blood and secreted by the male genital glands (testes or ovo-testes). In some cases the individual, although an undoubted male, has shown certain feminine characteristics as in the well-known case described by Haeckel(5) of a Greek gynecomast—a twenty-year old recruit with a small rounded face; he had neither beard nor moustache, and his photograph shows a sloping feminine contour of the shoulders. At other times there is a considerable growth of hair on the face and pectoral regions, and the general shape and aspect of the body is masculine. The stimulus to the growth and secretion of the mammary glands in the male is, however, not necessarily or solely of the nature of a hormone, for instance a case described by Alexander von Humboldt and quoted by Haeckel as being authentic. This was a solitary settler in a South American forest, whose wife had died in childbirth. "The man in despair had laid the newborn child on his own breast, and the continuous stimulus of the child's sucking movements had revived the activity of the mammary glands(5)."

Similar cases of male animals suckling their offspring have been reported in castrated sheep and in goats. The occurrence of functional mammae in castrated males suggests that an inhibiting influence is normally exerted by the male gonads on the development of the rudimentary female organs which are always present in the male sex. Should the testes be excised, or their

internal secretion be impaired by disease or degenerative changes, secondary female characters such as the development of fat and the enlargement of the normally abortive mammae, may manifest themselves.

Such an explanation has recently been advanced by Rogers Brambell(1) with reference to the development of female characteristics in hermaphrodite pigs. In the right gonad of one of these animals he has demonstrated the presence of ovarian tissue covered by germinal epithelium and containing oöcytes and primordial follicles; this tissue lay on the surface of the testis, and was separated from the semeniferous tubules of the medulla by the tunica albuginea. A cortical zone of spermatic tubules was present between the tunica albuginea and ovarian tissue, which was intermediate in character between the medullary and ovarian tissue. Many of the tubules in this region contained true oöcytes. Brambell explains the structure of these gonads by postulating a slight delay in the development of the male determining stimulus, which in male embryos normally takes place at an earlier date than the appearance of sex differentiation in female embryos.

A somewhat similar case in the human subject was reported by R. Rutherford(10) at the meeting of the Anatomical Society of Great Britain and Ireland in May 1929. In this case the child was so feminine in appearance, that when he was brought to the Padre for christening, the latter mistook him for a girl. An operation for undescended testis in the left inguinal canal revealed a well-developed uterus and Fallopian tube. A part of the Fallopian tube with the testis was removed, and these were afterwards examined microscopically. Tubules containing cells similar to those described by Brambell in the ovo-testis of an hermaphrodite pig were present in the tunica albuginea, and in the subserous layer, where the visceral layer of the tunica vaginalis was reflected from the mediastinal border of the gland.

In considering these cases care must be taken to distinguish between (1) the influence of the gonads or genital cells in producing the normal differentiation of sex in embryonic life and (2) the influence or absence of influence of the gonads on such an organ as the male mamma, at puberty or in the adult. In the first, the stimulus to the development of one sex appears to antagonise and suppress the development of the other. In the second case one may suppose (*a*) that some qualitative change has taken place in the secreting cells of the genital glands, or (*b*) that, in the cases of functioning mammae in male animals which have been castrated, or in which the internal secretion of the gonad is diminished or impaired as the result of disease, the suppressed elements of the recessive sex have been enabled to assert themselves.

The variations in development of accessory mammae and nipples from a simple papillary type to a fully developed and functioning organ have been amply described by Mitchell-Bruce(9) and other writers. The relative frequency of their appearance in the male and female, and the variations in their position have also been fully recorded and commented on by the same authors.

It is necessary, however, to discuss the supposed absence of heredity in the

occurrence of supernumerary mammae. Mitchell-Bruce obtained no family history of the presence of accessory mammae in relatives of the cases which he reported. These were 315 specially examined for their presence; 207 were males and 108 females. Among the 207 males 19 showed accessory mammae or 9·11 per cent.; 108 were females of whom 5 had accessory mammae or 4·6 per cent. No history of accessory mammae in the relatives of these 24 individuals was obtained. On the other hand Edwards, Cameron, Robert, Handyside and others have described cases in which a sister or parent has had an accessory mamma. In Dr Robert's case quoted by Cameron and by Hirst and Piersol, there was a well-formed functional mammary gland on the outer surface of the left thigh 4 inches below the trochanter. The mother of this woman had three mammary glands—one on the left side of the chest and two on the right. It seems probable, that as many cases of the papillary or areolar type are not noticed or considered to be of any importance even by the individual who possesses them until attention is drawn to them by some accident, or their enlargement during pregnancy, these individuals would naturally not know of their presence in relatives, and consequently the number of cases recorded of the presence of an hereditary factor would be considerably less than the true number.

SUMMARY

1. Description of a supernumerary mamma in the left axilla of an excessively fat man.

2. An account of the histological appearances of the mammary gland and testicle.

3. A comment on the influence of heredity in preserving structures in a rudimentary condition in one sex, which are normally fully developed and functional only in the other sex; with especial reference to the presence of mammary glands in the male.

4. A reference to the supposed inhibitory influence of the male gonads upon the development of the rudimentary mammae and other organs of the female generative system which are normally present in the male sex.

In conclusion I wish to express my thanks to Prof. D. M. Blair for his kind interest and assistance; to Mr J. Weston for the preparation of the microscopic sections, and Mr D. A. Kempson who photographed the specimen, and sections.

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A NOTE ON A RARE TYPE OF PTERION IN THE GORILLA

By M. F. ASHLEY-MONTAGU

There exists at the present time a certain amount of confusion concerning the structure of the pterion in the Primates. This is due in the first place, to the paucity of the number of observations which have been made upon this region, and in the second place, to the looseness with which some anthropologists and others have generalised upon the basis of a few cases in which one or another type of articulation may have been found.

Anoutchine, Ranke, Oppenheim and, recently, Collins and Hecker, have investigated this region in the skull of the Anthropomorpha, and their conclusions, on analysis, are found to be in substantial agreement. All agree that the pterion is exceedingly variable in its conformation in the Primates, and that it is quite impossible to assert, in the present state of our knowledge, that one or another type of pterion, with the exception of the Lemuroidea and the gorilla, is peculiar to one or another family or even sub-species. This statement, on the basis of my, as yet uncompleted, researches in this field, I believe, may be accepted as broadly true.

It would seem that the form of the pterion in which the alisphenoid articulates with the parietal bone, thus excluding the frontal from contact with the temporal bone, is present in about 80 per cent. of cases in the gibbon, 70 per cent. in the orang, 14 per cent. in the chimpanzee, and 0 per cent. in the gorilla. In the case of the gorilla, each of the above-named investigators uniformly found the fronto-temporal type of pterion in every one of the gorilla skulls examined by them. This fact led the latest investigator, Hecker, to assert that the fronto-temporal pterion was a constant feature of the gorilla skull—an opinion which is shared by all authorities who have written upon this subject. It is of the greatest interest, therefore, to be able to report a case of the occurrence of the parieto-sphenoidal articulation in the gorilla.

I have examined altogether 137 gorilla crania in which the pterion was visible on both sides of the skull. In 10 cases I found the point type of articulation, in which all four bones meet at a common centre, on both sides, whilst in one case I found the parieto-sphenoidal type of articulation on both sides[1].

The skull which is the subject of this note is in the collection of the Museo Nazionale di Antropologia e Etnologia, Firenze, and numbered 5362. The skull is that of a young female(?) in which M3 has not yet completely erupted.

[1] In a communication to me Mr J. B. Collins reports the occurrence of the parieto-sphenoidal articulation in two female gorillas, United States National Museum, Washington, No. 25276 s.p. right side only; No. 25278 s.p. left side only.

Fig. 1. Right side of gorilla skull showing parieto-sphenoidal contact.

Fig. 2. Young gorilla skull displaying the normally short type of alisphenoid.

The maximum length is 140 mm., and the breadth 103 mm. The breadth from pterion to pterion (bi-pteric width) is 80 mm. The length of the lip of the parietal bone at the pterion is 7 mm., and of the alisphenoid 11·5 mm. on the left side. On the right side the length of the parietal lip is 8·5 mm., and of the alisphenoid 9 mm.

There can be no question of an epipteric bone, for with the aid of a binocular microscope I was unable in this case to detect any inconsistency in the texture of the bone which might have led to the recognition of a pre-existing suture. As may be seen from the photograph, fig. 1, the actual form of the pterion is essentially of the human type, the alisphenoid reaching upwards to meet the retreating parietal. In most other gorilla crania which I have examined, the alisphenoid was appreciably lower upon the side of the skull, as may easily be seen to be the case in the young gorilla shown in fig. 2.

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ABNORMAL DUODENUM

By Capt. B. S. NAT, M.B., Ch.B., F.R.C.S., I.M.S. and
P. D. MOOKERJI, L.M.S.

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This abnormality was observed in the dissection room of the King George's Medical College, Lucknow in 1927. The age of the subject was about 50. Nothing is known about the clinical history or the cause of death.

DESCRIPTION

The following are the conditions exhibited by the abnormal duodenum:

First part (1, fig. 1). Measures 3·4 cm. Ascends to the right towards the gall bladder and is stained by bile. It is slightly dilated and the pyloric constriction is well marked.

Second part (2, fig. 1). Descends with a convex margin to the right and a concave margin to the left. The convex right margin is 10·2 cm. long. The head of the pancreas and the gastro-duodenal vessels lie along the concave margin.

Junction of the second and third parts. Shows a distinct constriction, which is placed at right angles to the axis of the gut. At this point the gut abruptly changes its direction, from a downward and inward course to a downward, outward and backward direction.

Third part (3, fig. 1). From the bend mentioned above, it takes a course as follows: The first 7·2 cm. (*a*, fig. 1) course downwards, backwards and to the right. The next 9·4 cm. (*b*, fig. 2) pass upwards, lying postero-lateral to the right margin of the second part. The following 10 cm. (*c*, fig. 2) passes transversely across the vertebral column, behind the second part and the head of the pancreas. This part is separated from the second part by a wedge-shaped outgrowth of pancreatic tissue, in front of which the common bile duct courses downwards and to the right and opens normally on the postero-medial aspect of the second part.

At its very commencement, this part is narrowed by a constriction, more marked on its inferior edge. This constriction can be traced in the form of a spiral to the posterior surface of the more distal portion, which is rather narrow in lumen. The constriction, therefore, unlike the one mentioned before, is not at right angles to the long axis of the gut.

The terminal portion ascends to end in the duodeno-jejunal flexure in its normal position.

Fig. 1. The duodenum as seen from the anterior aspect. The stomach is lifted up to expose the duodenum. Below is a pancreatic lobule overlapping the duodenum.

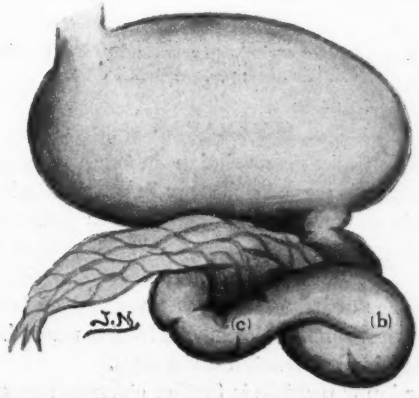

Fig. 2. Posterior aspect. The part marked (*c*) lies in front of the aorta. Only the terminal portion of this part can be seen from the front.

Associated conditions

The pancreas is larger than normal. Its head is situated against the concavity of the second part of the duodenum. From the posterior surface of the head a thin wedge-shaped mass passes to the right between the second and third parts. The rest of the posterior surface of the head with its uncinate process lies in front of the distal narrower portion of the transverse part, which therefore separates it from the aorta. The superior mesenteric vessels lie in front of the lower part of the head of the pancreas in the grooves on its uncinate process, which separates the mesenteric vessels from the duodenal wall. The bile duct opens normally on the postero-medial aspect of the second part of the duodenum. The wedge-shaped mass of the pancreas mentioned above separates it from the third part. The stomach is enlarged and dilated. Its longest diameter is 24 cm. and the vertical distance between the fundus and the greater curvature is 14·3 cm.

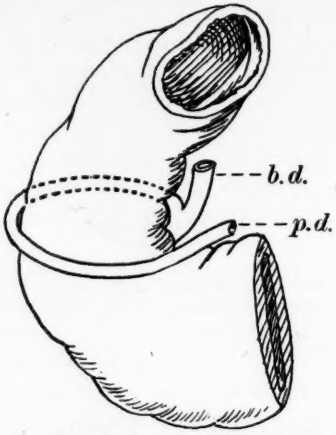

Fig. 3. Pancreatic duct encircling the second part of the duodenum.
b.d. bile duct; *p.d.* pancreatic duct.

REMARKS

The presence of the spiral constriction on the wall of the transverse part of the duodenum which is placed obliquely in relation to its long axis, unlike an ordinary stenosis or constriction ring which is generally at right angles to the axis of the gut, suggests a rotation of that part of the gut on its own axis. Developmentally, the rotation of the U-shaped loop of the midgut, whereby the right face of its mesentery comes to look towards the left and anteriorly in the adult, probably produces a torsion round its own longitudinal axis in the more proximally situated duodenum.

That such a torsion is possible is further strongly suggested by the report of a case in the *British Journal of Surgery* (vol. x, p. 318) by John Anderson,

in which the pancreatic duct encircles the second part of the duodenum before opening into it, as is shown in fig. 3. This can only be explained by a complete clockwise torsion of the gut on its own axis. Such a torsion of the duodenal wall can explain the abnormality described here.

Granting the presence of this torsion effect on the duodenal wall, how are we to explain the absence of any of these effects in a normal case. It is possible that the pressure of the superior mesenteric vessels together with the mesenteric pedicle against the duodenum, as they cross its third part as a result of the rotation of the gut, has a hindering effect on this tendency to axial rotation in a normal case. When the mesentery becomes secondarily attached to the posterior abdominal wall this pressure of the mesenteric pedicle on the duodenum will naturally be considerably relieved. This secondary attachment in a normal case takes place long after the rotation and retraction of the U-shaped loop. Thus the pressure is effective at a time when the rotation of the gut is tending to produce an axial torsion on the duodenal wall. If this adhesion takes place earlier than it ought to, that is, before or at the time of rotation of the U-shaped loop, the "mesenteric pressure" on the duodenum will be relieved earlier, thus allowing the torsion effect of rotation to reach the more proximal duodenal wall. In other words, the abnormality may be traced to a disturbance of the normal time-relation between the rotation of the gut and the adhesion of the mesentery. That this may be so is rendered probable by the fact that the superior mesenteric vessels in this specimen nowhere come into relationship with the duodenal wall.

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THE BRAIN OF FOSSIL ANIMALS[1]—A REVIEW

DR ARIËNS KAPPERS, *Amsterdam*

ALTHOUGH the preservation of the actual brain in a fossil state is of rare occurrence yet it is convenient to do as Dr Tilly Edinger has done and use the term "fossil brain" to indicate a cast made of the interior of a skull by nature. It is chiefly in this sense that she has employed the term in her important monograph entitled *Die Fossilen Gehirne*. She has rendered Neurology a great service by bringing together the scattered literature which bears upon the interpretation of natural and artificial endocranial casts and at the same time adding much that is new from her own investigations.

In her preface Dr Edinger informs her readers that she has written her treatise on *Paleoneurology* for the same reasons as her father Prof. Ludwig Edinger prepared the first edition (1880) of his well-known lectures on Comparative Neurology. Like him, she has been conscious of the many gaps in the branch of science which she has worked over and made her own. She pays a just tribute to Marsh and to Cope and to the interest roused by their work in the seventies and eighties of last century. In every chapter Dr Edinger proves her familiarity with the literature of her subject and gives evidence of an impartial judgment in estimating the scientific value of the many contributions which have been made to it.

At the beginning of her monograph Dr Edinger draws attention to the fact that a "fossil brain" is rarely found alone; it is part of a cranial fossil. The delicate tissue of the brain does not, in a mineral state, retain its structure as does a bone; its substance is completely replaced by inorganic matter. The structure or cast thus formed is moulded to fit its endocranial chamber. It sometimes happens as in the skulls of recent Halicores, found on the coast of New Guinea, that the cast is moulded not within the bone but within the dura mater of the skull. This was apparently also the case in the fossil casts of *Halianassa* described by Studer; in these casts there is no indication of meningeal vessels. A thin layer of calcareous matter, 2 mm. thick, represents the dura mater. On some "fossil brain" casts there is a covering of iron-oxide but this does not represent the dura; it is a deposit formed between endocranial cast and the containing bony walls[2]. Such a deposit usually forms only a thin layer. The replacement of the brain by the deposition of inorganic matter takes place slowly and often very incompletely.

Dr Edinger enters fully into the merits and demerits of the methods employed by anatomists for obtaining casts of the interior of skulls. She enumerates the substances employed—plaster of Paris, Jaekel's mixture (silica, chalk, gelatine, glycerine and lysol) and the substance used in the prosectorium of the Zoological Gardens, London—a mixture of glycerine, gelatine and zinc-white. The plaster of Paris method has many defects—especially the difficulty of obtaining accurate contours of recesses. For this reason she prefers mixtures in which gelatine forms the chief constituent. Poller's hydrocolloid negocoll deserves mention. I saw excellent casts made in Vienna with this substance; and equally delicate ones were obtained by van Ledden Hulsebosch in Amsterdam, who used this substance;

[1] *Die Fossilen Gehirne*. By Dr Tilly Edinger, Frankfort a. M., pp. 249, 203 figs. in text. (Berlin: Julius Springer, 1929.) Price 36 marks. Reprinted from *Ergebnisse der Anatomie und Entwicklungsgeschichte*, 1929, Bd. XXVIII, Abth. III.

[2] In man the dura mater is fixed to the cranial wall so intimately that bone and dura may be regarded as parts of the same stratum. It is otherwise in many of the lower animals where the dura is separated from the lining periosteum of the cranial bones.

his endocranial casts retain exact impressions of the most complex extensions of the cranial cavity.

Two beautiful photographs are given by Dr Edinger of the "brain" of a cave bear (*Ursus spelaeus*). They were made by taking a photograph (negative) of the interior of the skull and then printing from a diapositive of the negative.

Dr Edinger does not deny the possibility of brain substance becoming mineralised and thus preserved, but after discussing the petrified brains described by Hindze, she comes to the conclusion that these specimens must be regarded as silicate artefacts. Brain ganglia of Invertebrates are rarely preserved; even those of cartilaginous fishes are very uncommonly met with in geological deposits. In ossified skulls, "brain-casts" are not uncommon. Such casts do not give the real volume of the brain; this is particularly true in the case of fish but it is also true in the case of man. For calculating the brain volume of man—from endocranial casts—Dr Edinger gives Welcker's formula. This formula cannot be applied to the endocranial casts of mammalian skulls unless the age of the animal, thickness of meninges and the spaces between and within the meninges are taken into account. The perimeningeal tissues are very thick in some animals, to such a degree that the volume of the endocranial cast may be several times the size of the actual brain (see p. 33). In the controversy concerning the interpretation of the convolutions and fissures of the human brain from endocranial casts raised by the late Prof. J. Symington, Dr Edinger takes the side of Boule, Anthony and Elliot Smith, but is careful to give all the pros and cons which must be taken into consideration. Personally I am convinced that Symington greatly exaggerated the difficulties of interpretation and I share the opinion of Boule, Anthony, Elliot Smith and Keith. There are instances in which we may observe the actual course of principal fissures on endocranial casts of prehistoric human skulls. My observations made last year on ten "prehistoric" casts (that of *Pithecanthropus* being included) has convinced me that we may thus obtain accurate pictures of the convolutions and fissures of the frontal lobe. The pictures presented by such casts agree so closely with actual specimens of the brain that I have no doubt about the reliability of the casts taken from the interior of prehistoric human skulls as giving a faithful reproduction of the convolutions and fissures of the brain of fossil man.

Dr Edinger cites Schwalbe's observations on the convolutionary impressions made on the skull by the brain—viz. that the *impressiones digitae* are confined to the basal, frontal, occipital and lower temporal parts. It is evident that the brain being slightly heavier than the surrounding cerebro-spinal fluid presses more on the basal regions of the skull, leaving the upper or parietal regions uncompressed and therefore unmarked by convolutions. In this connection Dr Edinger discusses observations of Sir Arthur Keith who called attention, in his report on the Galilee skull to the accumulations (*cisternae*) of cerebro-spinal fluid in the parietal and fronto-parietal regions of the skull and to the consequent absence of convolutionary impressions—independently of any question of the action of gravity. In Mammals, particularly Carnivores, all the fissures and convolutions, especially those of the parietal region of the brain, may be clearly reflected on the skull and even on the outer aspect—a fact to which Schwalbe called attention. The external manifestations of cerebral markings has also been investigated by Dr Edinger.

After this general introduction the author discusses the various forms of endovertebral and endocranial casts, starting with endosacral casts of *Morosaurus lentus* (fig. 32), *Apatosaurus ajax* and *Stegosaurus ungulatus* (fig. 33) by Marsh and *Kentrurosaurus æthiopicus* (fig. 34) by Hennig. All of these she compares with similar casts from recent animals.

Then she deals with all parts of the brain. Interesting is her statement that the largest animal of all times the dinosaur *Brachiosaurus* (examined by Janensch) had the largest hypophyseal recess ever observed in fossil skulls. Dr Edinger

believes that she has succeeded in showing that, as a rule, the size of the hypophysis bears a direct relation to the size of the body. This thesis, which Dr van der Horst made the subject of a research in my Institute, found to hold good in the majority of recent animals (e.g. *Struthio camelus* and *Zalophus californianus*, compared with smaller representants of their orders, not yet published). Still, there are cases, to which Dr Edinger refers, where this correlation is less evident.

The thalamencephalon and indications of the parietal eye and epiphysis have also been carefully studied and recorded.

Proceeding to the forebrain Dr Edinger discusses very fully Marsh's thesis concerning the size of the brain in relation to the size of the body—his "general law of brain-growth," about which also E. Dubois recently published such interesting data. Dr Edinger does not agree in all respects with Marsh's conclusions and points out that this correlationship does not hold good so much for the paleoencephalic parts as for the hemispheres, a result which was to be expected. In some forms, the cerebellum and olfactory lobes may even show a considerable decrease with enlargement of the body.

Later in her monograph Dr Edinger discusses Marsh's and Lankester's thesis that groups which in an early period had a relatively large brain had a longer duration than those in which the brain was originally rather small. Although she found that there are certain groups with long endurance which had large brains and that groups with a small brain usually disappear after a short period, yet there were others that, notwithstanding their small cephalisation, have existed over a very long geological period, while others, although large brained disappeared after a short history.

After giving her general introduction Dr Edinger proceeds to the systematic treatment of her subject—Paleoneurology. Beginning with fossil brains of fish she ascends the vertebrate scale, finishing with human examples. It would be impossible to summarise this part of her work; it is enough to say that it represents scientific work of the most painstaking kind. Dr Edinger's work is the most authoritative treatise on a subject she has made her own. I know of no other work which gives the literature relating to Paleoneurology so completely or so accurately. By publishing this work Dr Edinger has rendered a great service to science and has honoured the name she bears.

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